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ONTOGENY OF CAMERATE CRINOIDS[1]

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ABSTRACT

Relatively complete growth sequences are known for various camerates. In most cases, these range from young animals with four to eight brachials per arm and "sizes" of 1.0 to 1.5 mm to mature crinoids with 5.0 to 75 mm "size" and over 100 brachials per arm. Microcrinoid growth stages are known in one species, which is questionably assigned to the Camerata. These growth stages are closely comparable to those of living crinoids except that the plates joined earlier and the arm facets developed in a different order. Recent forms and the camerates show the same plate development sequence with one exception. The first interprimibrach in camerates appeared much earlier than the equivalent plate in modern crinoids. This is related to the presence of fixed brachials in the camerates which are lacking in living species. Camerate crinoid calyces can be subdivided into five types depending on the number of fixed brachials, interbrachials, and arms. Regardless of calyx type, the youngest camerates are all similar but the different types diverge throughout later ontogeny.

Columnal growth is uniform in all crinoids. However, the calyx plate and brachial ontogenies follow strikingly different paths in the camerates and Recent crinoids. In camerates, the axial nerve cords lay on the interior side of the plates throughout life. This configuration also characterizes the embryonic plates of Recent crinoids. During later growth, the plates of modern crinoids diverge from those of camerates and the nerve cords are gradually buried within the plates. The divergence is partially explained by the fact that all camerate calyx plates served the same functions; in modern groups, the various calyx plates are specialized to perform different functions. Contrasts in brachial growth are caused by different locations of the axial (aboral) nerve cord within the arms. In all crinoids, the pattern of growth for the radial plates dictates that of the brachials. The ultimate control of crinoid plate growth is believed to be mesodermal; for stem, arm, and ray plates, the mesoderm may act by means of the aboral nerve cords.

Throughout ontogeny, the length of the food-gathering system is augmented by means of addition of new brachials and pinnulars and height growth of previously formed plates. The food-gathering system of camerate crinoids grew much more rapidly relative to "size" and calyx volume than expected based on geometrical considerations. The ratio of the length of the food-gathering system to calyx volume decreased in older and larger crinoids. Differential natural selection is documented for several camerates. Natural selection reduced variation of the length of the food-gathering system with respect to calyx volume during ontogeny. The selection discriminated against animals with relatively short food-gathering systems.

A crinoid endoskeleton is a complex of supporting relationships. Basically, each plate

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supports all of the higher ones. For example, the proximal columnal supports the crown, whereas the distal fixed brachial bears the arm. Possibly critical ratios of the weight of the food-gathering system/area of supporting brachial and crown weight/area of proximal columnal serve as limits to growth.

INTRODUCTION

Despite the fact that growth sequences have been known in camerate crinoids for many years, only rare papers have treated the ontogeny of these animals. Several growth series are illustrated and briefly discussed in the systematic literature (e.g., Wachsmuth & Springer, 1897; Goldring, 1923). Detailed papers on development include qualitative studies by Koenig (1965) on the platycrinitid *Cyttarocrinus eriensis* (Hall), Meyer (1965) on platycrinitid radials, and Laudon (1967) on *Platycrinites bozemanensis* (Miller & Gurley). Macurda (1968) presented a quantitative study on the ontogeny of two species of *Eucalyptocrinites*. This report is principally based on my statistical investigation of six camerates from the Girardeau Limestone (Late Ordovician) (Brower, 1973).

The only growth stages of pre-brachiate ("microcrinoid") camerates known are those questionably assigned to the platycrinitid *Cyttarocrinus eriensis* (Hall) (see Koenig, 1965). The young crinoids range from about 0.2 to 1.5 mm in calyx height. The smallest specimens lack arm facets but the observed oldest developed arms on all radials.

Aside from the questionable species just mentioned, the smallest known camerates are about 1.0 to 1.3 mm in "size" (consisting of height from the calyx base to the distal primaxil level) and possess four to nine free brachials in each arm, most with well-developed pinnules. The primibrach *1* and in some individuals the primaxil are incorporated in the calyx. The microcrinoidal and the earliest growth stages with arms are absent. Mature camerates range from 5 mm to several cm in "size," have 50 to several hundred free brachials in each arm, and are characterized by varying numbers of fixed brachials.

A Recent crinoid crown consists of an internal skeleton composed of a series of adjacent calcite plates. The endoskeleton is mesodermal and occupies the major part of this layer. The outer plate surfaces are covered by a thin epidermal layer, which is not completely developed in some specimens. Plates of the calyx comprise most of the body wall which encloses the viscera of the crinoid (see Hyman, 1955, p. 47-61, for summary).

In simple statement, three processes are seen in Recent and fossil crinoid ontogeny: 1) development of new plates, 2) calcite accretion and increase in size of previously formed plates, and 3) complete or partial resorption of plates.

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TERMINOLOGY

Generally, terminology employed here follows standard *Treatise* practice for camerate crinoids. Plates located between adjacent rays are called interprimibrachs. Plates occurring within a single ray comprise intersecundibrachs, intertertibrachs, etc. The designation lateral interrays includes the *AB, BC, AE,* and *DE* interrays.

One of the major problems in relative-growth studies is determination of a standard parameter for relative age. For camerate crinoids, the most satisfactory measure is "size" which consists of height of the calyx, measured from its base to the distal margin of the primaxil (primibrach 2, Brower, 1973, p. 290). Throughout this paper, "size" refers to this measurement whereas size, lacking quotation marks, denotes size in a general sense. The growth rate of "size" is not constant with respect to time. Living and fossil crinoids are characterized by growth rates of "size" that are slow-fast-slow, i.e., "size" growth with respect to time is slow in young and adult individuals, but juvenile animals show comparatively rapid developmental rates. Consequently, "size" measures only relative age, not absolute chronological age.

The standard brachial measurements and terminology are illustrated in Figure 1.

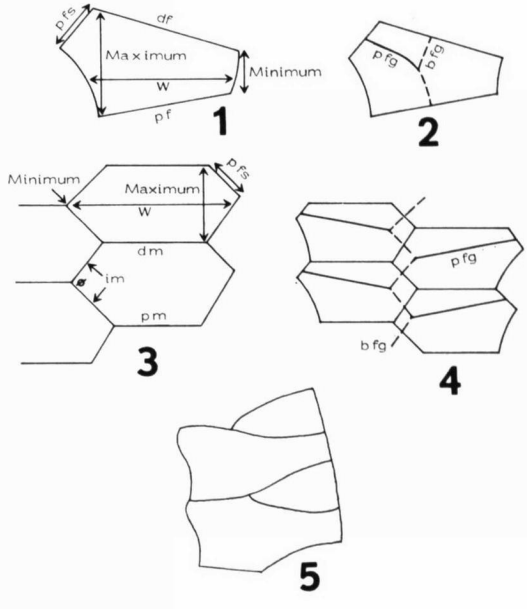

FIG. 1. Diagrams illustrating brachial terminology (Brower, 1973).——*1.* Uniserial brachial, dorsal view showing measurements and terms [*pf* and *df*, proximal and distal faces; *W*, width; maximum, greatest height; minimum, least height; *pfs*, pinnule facet size. Convergence angle is measured between proximal and distal faces].——*2.* Uniserial brachial, ventral view with food-groove-axis designations [*bfg*, brachial food groove; *pfg*, pinnule-facet food groove].——*3.* Mature biserial brachials, dorsal view [symbols as in *1* except: *im*, inner margin; *dm* and *pm*, distal and proximal margins (note differentiation of inner from proximal and distal margins); Ø, convergence angle, always measured between inner margins or their equivalents, minimum height of biserial brachials always zero].——*4.* Mature biserial brachials, ventral view [food-groove legend as in *2*].——*5.* Oblique sketch of immature biserial brachials, pinnule facets only shown on left side. Note lack of differentiation of inner vs. proximal and distal margins.

SEQUENCES OF PLATE GROWTH

Among Recent crinoids complete sequences of plate growth can be observed directly. In camerates, this applies only to the later developmental phases, since earliest sequences must be

inferred. During the growth of most camerates, free brachials were incorporated into the calyx, although at variable rates. This does not occur in modern crinoids or in inadunates and flexibles, where the arms remained free above the radials throughout life. Making allowance for the development of fixed brachials and correlated characters, the plate-development sequences of camerates and modern crinoids are almost the same, especially with respect to arms and column. In many living comatulids, the animal discards its column at the end of the pentacrinid growth stage and assumes a more or less free-living existence. This does not occur in camerates and Recent isocrinids, where (barring traumatic accidents) all or part of the column is retained until death. Despite this difference, growth of the comatulid larval column and the camerate and isocrinid stem follows the same pattern.

With the exception of *Cyttarocrinus eriensis* (Hall) (see Koenig, 1965, p. 406-412) (Fig. 2), nothing is known of early growth stages in camerates. Koenig examined several hundred specimens 0.2 to 1.5 mm in cup height, which he assigned tentatively to *C. eriensis*. However, Hall's holotype is 3.2 mm high and there is a size gap where no specimens are known. Consequently, it is questionable whether *C. eriensis* and Koenig's growth series of microcrinoids are conspecific, although two lines of evidence suggest that the growth sequence and the holotype of *C. eriensis* are conspecific. First, the microcrinoids exhibit elliptical column facets as does the holotype of *C. eriensis,* and secondly, the shape of the calyx of the largest microcrinoids resembles that of the holotype. Pending statistical study, I assume that all of these specimens represent *C. eriensis,* which is assigned to the Hapalocrinidae of the Platycrinitacea. The youngest crinoids possess the basals, orals, and radials which lack arm facets; all plates are completely

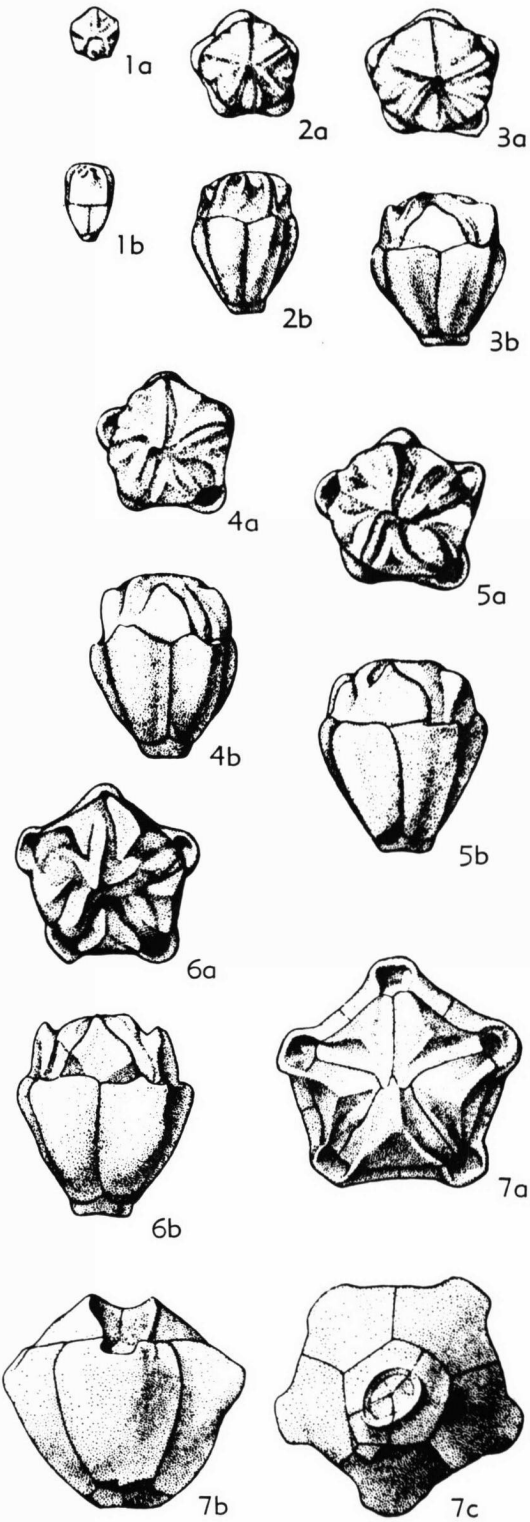

FIG. 2. Ontogeny of the platycrinitid *Cyttarocrinus eriensis,* Middle Devonian, New York, USA (Koenig, 1965). The *a* series of drawings are tegminal views with the *CD* interray directed downward; the *b* series are side views of the *CD* interray, except *7b* in which the *C* ray is central.——*1a,b; 2a,b.* Specimens with no arm facets, ×25.——*3a,b.* Specimen with *C* ray arm facet, ×25.——*4a,b.* Specimen with arm facets on *C* and *E* rays, ×25.——*5a,b.* Specimen with arm facets on *C, E,* and *B* rays, × 25.——*6a,b.* Specimen with arm facets on all radials except *A,* ×25.——*7a-c.* Specimen with all arm facets, ×15.

joined together. The largest *Cyttarocrinus* specimens retain the same plate structure except that all five arm facets are seen and the proportions of the various plates relative to each other have changed. The arm facets are, listed from first to last appearance: *C, E, B, D,* and *A*. During growth, each arm was separated from the next one by an angle of about 144°, and the new arms grew on every other radial until all were present. This minimized the lateral displacement of the center of gravity of the crown while the new arms were initiated. For example, if new arms grew on adjacent radials, the center of gravity would have shifted toward the two adjacent radials. The crinoid need only have genetically programmed the first arm to develop along with a 144° separation of subsequent arms. These two specifications would have dictated the sequence of all arms. Koenig (1965, p. 411) noted that new elliptical columnals grew immediately below the calyx with one columnal forming along with each arm. The long axis of the columnal lay at roughly 90° to the axis of the radial on which the arm was initiated. Consequently, the columnal was oriented to allow the calyx to counterbalance the added weight of the new arm along a pivotal joint, i.e., the long axis of the elliptical columnal. The placement of the long axes of the columnals could have been genetically programmed by the same formula used to develop the arm sequence. Koenig (1965, p. 400) believed that the primanal appeared along with the last-developed arm. The plate has not been seen and this cannot be verified. However, the 0.52 mm-high crinoid (Fig. 2,*2*) exhibits a notch between the *C* and *D* radials, and possibly the plate was initiated at this time, before any arms appeared.

The ontogenetical sequence of *Cyttarocrinus eriensis* is somewhat similar to that of Recent crinoids (compare Fig. 2 and 3; see Table 1). The ranges of calyx heights are comparable, as are the general sequences of plate development and changes in calyx shape. The most striking contrasts are: 1) the sequences in which the arm facets develop differ; 2) *Cyttarocrinus* plates are joined much earlier during ontogeny; 3) contrasts of growth in the individual plates appear as later annotated.

Aside from *Cyttarocrinus eriensis,* the youngest known camerates have "sizes" ranging from 1.0 to 1.3 mm and bear four to nine free brachials in each arm. The youngest ontogenetic phases must be inferred statistically. By analogy with living species, monocyclic camerates possessed two growth stages of "microcrinoids": 1) basals + orals; 2) basals + orals + radials. Similarly, three "microcrinoids" may be predicted for dicyclic camerates: 1) basals + orals; 2) basals + orals + infrabasals; 3) basals + orals + infrabasals + radials. These can be estimated by selected equation values taken from regression lines such as "size" *(X)* vs. fixed brachials *(Y)* and radial height *(X)* vs. "size" *(Y)* for selected camerates. The initial intercepts of the equations of "size" *(X)* vs. the various plate dimensions *(Y)* suggest the development sequences of plates. The process assumes that 1) regression lines yield good fits to the data, and 2) the "microcrinoids" grew according to the same relationships observed in older and larger crinoids. This hypothesis cannot be verified for the camerates because the "microcrinoids" are not known, but it seems to hold true for the Recent crinoids studied. Further details are given by Brower (1973, p. 305-310).

At worst, study of the "microcrinoids" constitutes merely a statistical exercise. At best, they have biological significance and outline the rough "sizes" of these growth stages for the camerates examined. I favor the latter view. At any rate, comparisons of the "microcrinoid" values for Girardeau camerates and Recent comatulids indicates that all are similar (Table 1).

The early sequences of plate initiation have been calculated wholly or partially for various Girardeau camerates. The following sequence of plate growth, listed from first to last appearance, characterizes all taxa: basals, infrabasals (if present), radials, primibrach *1,* primibrach *2* (primaxil), secundibrach *1,* and so forth. The orals have not been seen in the Girardeau fossils. Nevertheless, the above-listed plate sequence exactly parallels that of Recent comatulids. Presumably, the camerate orals formed in the same order as those of extant species.

Typically, the proximal interprimibrachs of Recent crinoids develop late in ontogeny. For example, they are first seen after the primibrach *2* (primaxil) is well defined in *Comactina meridionalis* (Fig. 3), but the interprimibrachs of *Promachocrinus kerguelensis* do not appear until about five secundibrachs are present. Generally,

TABLE 1. *Microcrinoid Values.*

	BB + OO "size" mm	BB + RR + OO "size" mm	First appearance of IIBrr "size" mm
MONOCYCLIC CRINOIDS			
ARTICULATES			
Comactina meridionalis	....	0.17–0.27	0.98
Hathrometra sarsii	0.27	....	IIBr6 at 0.58
Antedon bifida	0.26–0.32	....	....
Hathrometra prolixa	0.22–0.27	0.42–0.48	about 1.4
CAMERATES			
Eopatelliocrinus scyphogracilis	0.11–0.17	0.22–0.63	0.29–0.56
E. latibrachiatus	0.16–0.33	0.39–0.63	0.34–0.77
Macrostylocrinus pristinus	0.10	0.23–0.63	0.28–0.83
Alisocrinus tetrarmatus	anomalous	0.50	0.22–0.57
Cyttarocrinus eriensis ?	less than 0.2	0.2 –0.52	....

	BB + OO "size" mm	BB + OO + IBB "size" mm	BB + OO + IBB + RR "size" mm	First appearance of IIBrr "size" mm
DICYCLIC CRINOIDS				
ARTICULATES				
Antedon adriatica	....	0.10	0.25	....
Promachocrinus kerguelensis	....	0.12–0.15	0.15–0.41	0.80

the living crinoid radianal forms earlier than interprimibrach *1*, ranging from just prior to soon after appearance of the radials.

I believe that the radianal and proximal interprimibrachs of living crinoids are homologous with the primanal and proximal interprimibrachs of camerates, as evidenced by similarities of topographic position, ontogeny, and phylogeny (Brower, 1973, p. 301-304). The same changes occur during the ontogeny of *Comactina* and allied forms and in camerate phylogeny. For example, in the evolution of *Rhaphanocrinus* to *Ptychocrinus*, the basic change is displacement of the interprimibrach *1* from between adjacent radials to a position between the primibrachs *1* of adjacent rays, and above the radial circlet. A very similar change occurs in growth of *Comactina* (Fig. 3). The situation with respect to the radianal is almost identical.

At present, adequate interprimibrach data are available only from the Girardeau camerate *Alisocrinus tetrarmatus* Brower (1973, p. 408-432) where the interprimibrach *1* was probably initiated along with or immediately after the radials. Most likely, the *Alisocrinus* primanal (believed homologous with the radianal of living species) formed at about the same time. Relative to modern crinoids, the *Alisocrinus* interprimibrach *1* is postulated to have appeared earlier, whereas the proximal plates of the *CD* interray of both camerates and Recent forms began at roughly the same time. Whether or not this pattern is typical of all camerates cannot be determined at present. The necessary initial intercepts have not been calculated for other taxa. However, the geometry of all camerates is consistent with early development of interprimibrach *1*. If so, the different developmental sequences of interprimibrach *1* between the camerates and living crinoids is clearly related to and correlated with the presence or absence of fixed brachials. The camerate fixed brachials are incorporated in the calyx by

FIG. 3. Growth stages of *Comactina meridionalis*, Recent, from Yucatan, Mexico (Springer, 1920). [Explanation: *an*, anus; *B*, basal; *IBr*, primibrach; *iR*, interbrachial *1*; *O*, oral; *R*, radial; *RA*, radianal.]

1. Prebrachiate stage theca consisting only of basals and orals. [Note highly porous plates not fully joined together.]

2. Slightly older specimen with embryonic radials and radianal.

3. Largest prebrachiate stage with radianal and all radials (radianal below and left of *C* radial).

4. Specimen with embryonic primibrachs (proximal plates fully joined but gaps between distal ones).

5. Specimen with well-developed primibrachs and embryonic interbrachials *1*.

6-8. Growth sequence of progressively older individuals. [Note distalward migration of radianal and interbrachials *1*.]

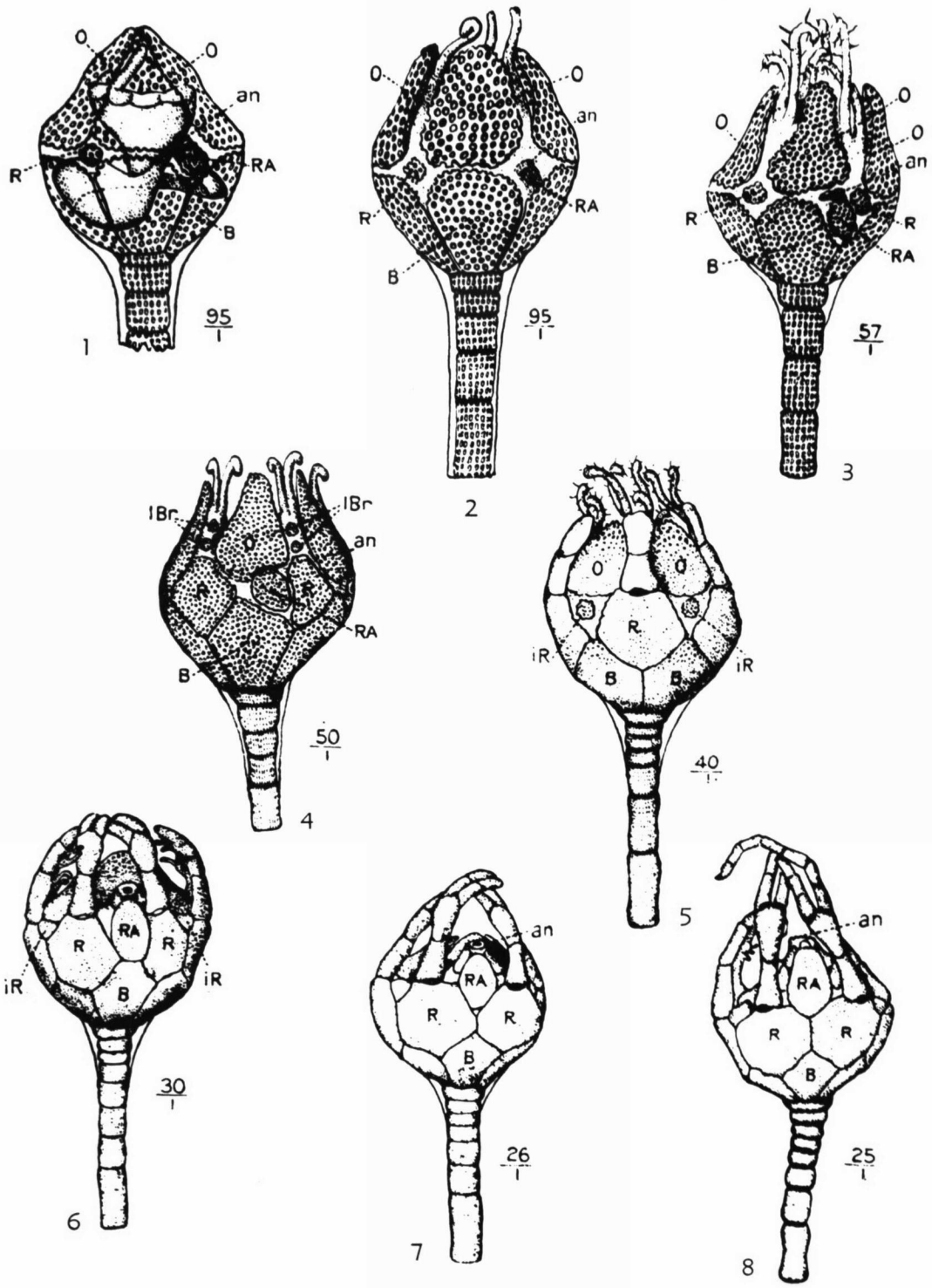

FIG. 3. *(For explanation see facing page.)*

interbrachials; Recent crinoids lack fixed brachials and the arms are free above the radials.

Some Paleozoic camerates developed only a few fixed brachials (e.g., platycrinitids and dichocrinids). These may or may not have retained the alisocrinid type of early interprimibrach *1* formation. However, the earliest growth stages of *Platycrinites bozemanensis* illustrated by Laudon (1967, fig. 1, 2) are suggestive of early development of interprimibrach *1*.

The development sequence of the stem and arm plates of living species and the camerates follows the same order. Columnals typically are introduced immediately distal to the calyx, below the centrodorsal in pentacrinid growth stages of comatulids and below the infrabasals or basals of camerates. Also new columnals are generally intercalated between previously formed plates of the stem.

All brachials and pinnulars first appear at the distal tips of the arms or pinnules. In modern crinoids, pinnules do not form until after the arms are well developed. The first pinnule of *Hathrometra sarsii* is seen when about secundibrach *14* is present; in *Antedon bifida,* pinnules occur along with secundibrach *12*. The first pinnules are formed at the arm tips; these are followed by the proximal (oral) pinnules on secundibrach 2. After these, the intervening ones appear. Pinnules developed earlier in camerates. The smallest known individuals with arms are about 1.0 to 1.3 mm in "size," possess four to nine brachials in an arm, and show a full complement of pinnules.

TIME-GROWTH OF LIVING AND FOSSIL CRINOIDS

Little is known about the life spans of extant crinoids, although the growth rates of plate circlets and size relative to time vary greatly among different species. In *Antedon bifida,* spawning occurs at the end of May or early June and the crinoid is ready to cast off the column and terminate the pentacrinid growth stage in mid-September (Thompson, 1865). Apparently *Hathrometra sarsii* reproduces in June and the pentacrinid stage is terminated by March through May of the next year. By far the slowest growth rates are seen in *Promachocrinus kerguelensis* which probably spawns around mid-September or early October. Individuals ready to discard the column are found in June. Based on data presented by A. H. Clark (1921, p. 530-537) and Fell (1966, p. 49), Brower (1973, p. 304-305) postulated that the microcrinoid and pentacrinid growth stages encompass about 20 months and that the animal lives about 15 years. Individual species are also characterized by wide variation in the growth rates of size and plate circlets with respect to time.

The few available data suggest that growth rates of size relative to time in modern crinoids fit a "slow-fast-slow" model. "Slow" growth rates seem to occur throughout the microcrinoid growth phase and well into the pentacrinid stage. Apparently, the "fast" growth is initiated just prior to loss of the column. When these growth rates are terminated is uncertain, but probably these end at or immediately prior to maturity. Older crinoids are characterized by "slow" time-size growth rates. The transition from the initial "slow" to "fast" growth rates is illustrated by Brower (1973, fig. 5). The change from the "fast" to the mature crinoid "slow" growth rates is indicated by two lines of evidence. Growth lines on fossil crinoid plates, where preserved, become more closely spaced toward the periphery of the plates. Assuming periodic growth lines, this denotes slower calcite deposition in older and larger crinoids. Initial growth lines of the "slow" phase are not preserved and only the growth lines of the "fast" and mature "slow" phases have been observed. Data presented by H. B. Moore (1935) denote that growth rings form seasonally in living echinoids. According to Clark (1915, p. 197-198), after the adult stage of modern crinoids is reached, the rate of brachial formation at the arm tips takes place at a constantly decreasing rate. During later growth, the brachial addition rate is "slow" and the general proportions of arms relative to the calyx is not substantially changed. Most size increase in adults occurs by means of calcite accretion to the previously formed plates. Similar growth rates of size relative to time are known for other echinoderms such as echinoids and starfish.

INTEGRATION AND COORDINATION

INTRODUCTION

The concept of integration and coordination is closely related to placement of the aboral or axial nerve cords. The axial nerve cords of mature *Antedon* are separated from the food grooves by calcite throughout the free arms. When these join the calyx, they penetrate and pass through the radial and then become connected to the chambered organ. The main aboral nerve plexus of *Antedon* lies under the basal rosette, partly beneath and beside the radial circlet and partly inside and above the centrodorsal (Nichols, 1962, fig. 2; fig. 4,*1*). The aboral nerves within the *Antedon* cirri and within the isocrinid stem originate at the base of the chambered organ.

Within the free arms, the aboral or axial nerve cords of a camerate lie at the base of the food grooves (Fig. 4, 5). These extend into the calyx at the arm openings where the aboral nerve cords are located along the plate interiors. In some species, the nerve cords were housed in grooves on the plate interiors, e.g., *Macrostylocrinus cirrifer* Ramsbottom (Fig. 6) and *Ptychocrinus fimbriatus* (Shumard) (the grooves correspond to ridges on the internal molds of the macrostylocrinids). Other crinoids, such as platycrinitids, lack these internal grooves and the aboral nerve cords apparently rested on the plate interiors (Meyer, 1965).

Study of internal and external molds of *Macrostylocrinus cirrifer* indicates that the external ornamentation (median-ray ridges and stellate ridges) developed directly over the internal aboral nervous system (Fig. 6,*1*). This is also seen in numerous other camerates, such as *Pytchocrinus fimbriatus,* which have thin plates in conjunction with well-developed ornamentation consisting of median-ray and stellate ridges. Thus, the approximate location of the aboral

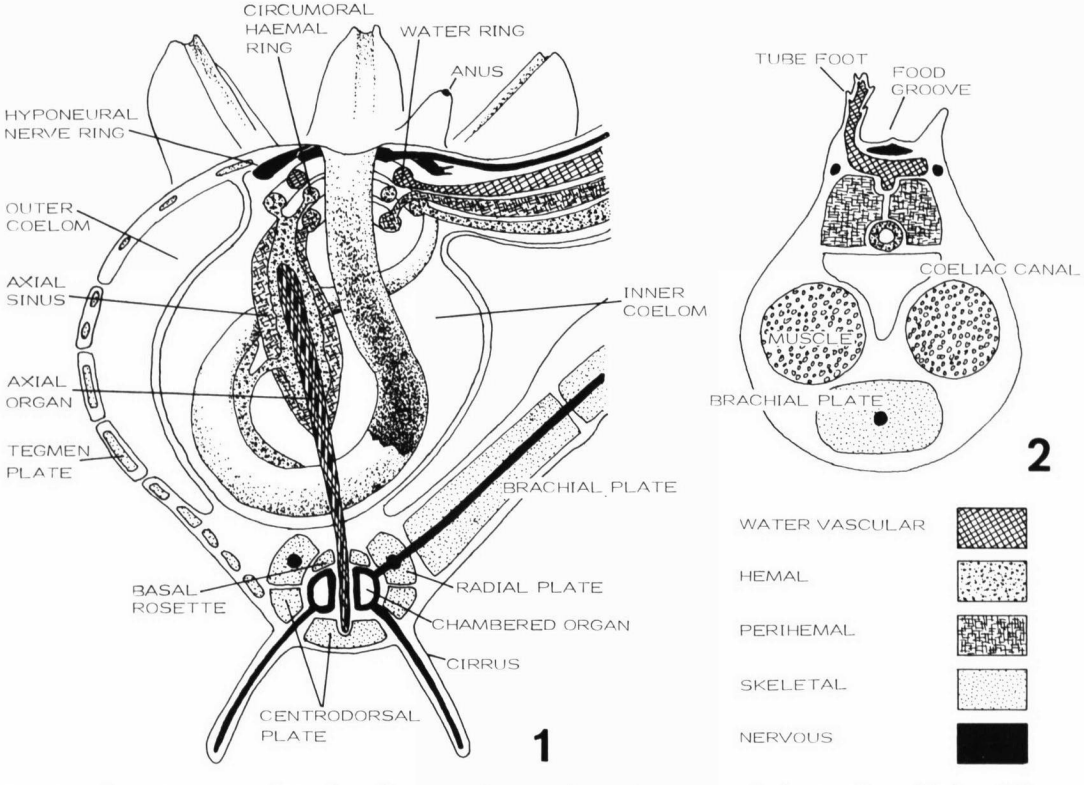

FIG. 4. Schematic cross sections through cup and arm of *Antedon,* Recent (redrawn after Nichols, 1962).——*1.* Side view.——*2.* Section through arm.

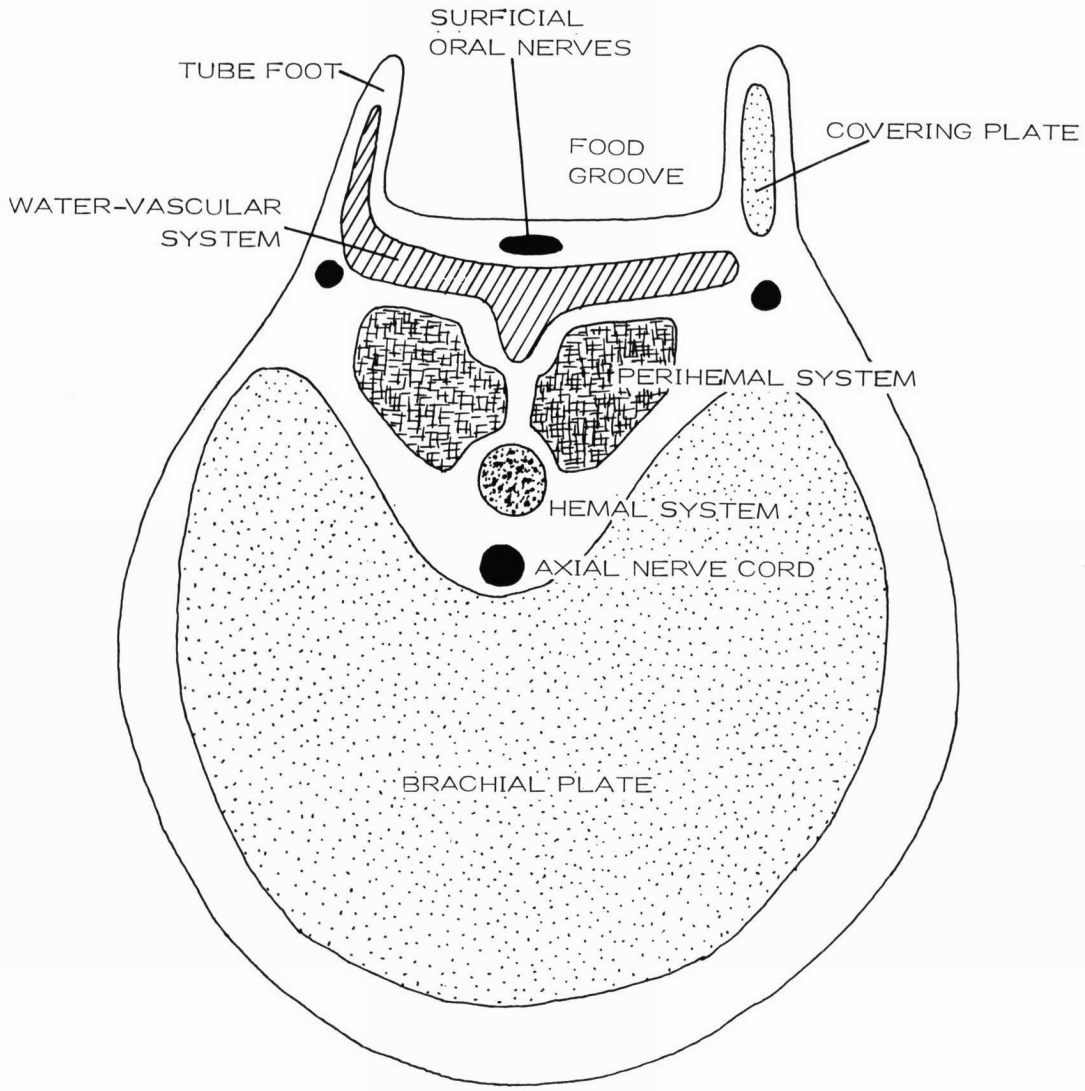

Fig. 5. Schematic cross section through camerate arm (Brower, n). [Symbols as in Fig. 4.]

nervous system may be ascertained by inspection of the external ornamentation.

It should be noted that the relationship between the aboral nerve cords and external ornamentation of basals of monocyclic camerates and of infrabasals of dicyclic forms is somewhat uncertain. The chambered organ probably was located mainly at the level of the basal circlet in monocyclic forms (see Brower, 1973, p. 363-371, for more details). Some of the external ridges on the basals seem to have corresponded to the lobes of the chambered organ, whereas others may have been associated with its interlobes (see *Macrostylocrinus cirrifer,* Fig. 6). An analogous situation most likely existed with the infrabasals of dicyclic camerates.

The configurations of the aboral nerve cords in camerates postulated above resemble those of Bather (1900, fig. 12) except that the distal extent of the chambered organ was probably higher.

OBSERVATIONS AND MECHANISMS

In the earliest growth stages of extant crinoids, the calyx plates are not fully in lateral contact.

They are isolated from one another by the soft tissues (Fig. 3). At this time, the plates commonly are arranged irregularly and the individual plates vary widely in size and shape (e.g., *Antedon bifida,* Clark, 1921, fig. 1181, 1189). This shows that the growth of a certain plate is poorly coordinated and integrated with other plates during this stage. Due to calcite accretion along the plate sides, the plates eventually join, except for certain "strategic holes," such as the arm openings, anus, and axial canal of the column. This ontogenetic pattern is probably dictated by the functions of the internal skeleton of calcite plates. Basically, the plates serve to support and protect the fragile organs housed on the inside of the skeleton. In extremely small and immature individuals of living species, the water-vascular system and other coelomic cavities probably provide the necessary support by hydrostatic means. However, with increasing size, mass, and volume, the ratio of the (volume of the coelomic cavities)/(total mass or volume) probably becomes too low to ensure the necessary support and this function is taken over by the skeleton. Although the earliest developmental stages are not known in any Paleozoic crinoid, presumably a similar pattern existed. Once the plates join, the support problem requires that this configuration be maintained throughout subsequent ontogeny. This probably simplifies growth of the plate mosaic, and it presents an approach to delineation of ontogeny. In general, if one plate increases in size, its neighbors must do the same. Otherwise gaps would appear between the adjacent plates and the skeleton could not support the animal. In other words, the development of all plates must be integrated and coordinated to prevent the formation of gaps. Matrices of correlation coefficients and covariances yield information on this type of integration and coordination. Progressive increase of plate and calyx size is denoted by positive correlation coefficients. Resorption would result in decreased size and

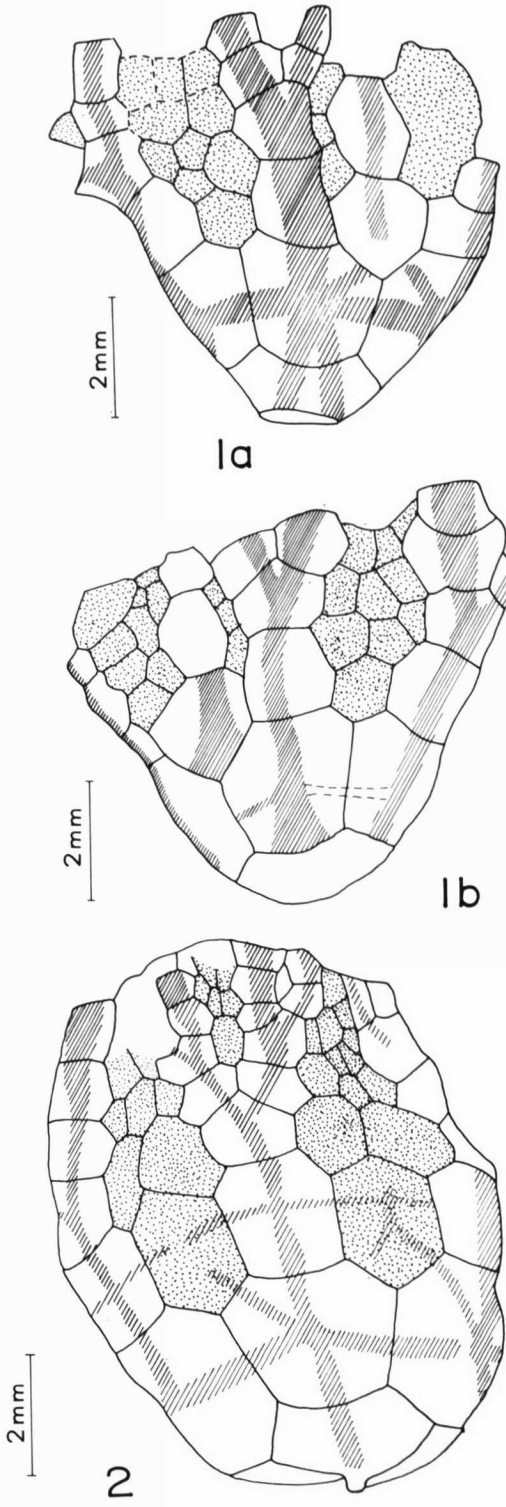

FIG. 6. *Macrostylocrinus cirrifer* Ramsbottom, Upper Ordovician, Scotland, showing traces of aboral nervous system (ruled) represented by ridges on internal molds and median-ray ridges on external molds (interbrachials stippled) (Brower, 1973).——*1a,b.* *C* ray, external and internal molds of holotype, showing correspondence of internal ridges to external ornamentation.——2. Side view of paratype (internal mold).

would be shown by negative correlations for the plate or plates affected. However, resorption was not common in Paleozoic crinoids except for the stem facet, arm openings, and possibly the anal opening. Integration and coordination gradients exist, and the dimensions of a given calyx plate correlate best with those of the directly adjoining plates and less well with plates farther away. These integration requirements apparently require or are simplified by linear growth. For example, in the Girardeau crinoids, all regression lines for the major calyx plates are linear (i.e., infrabasals, basals, radials, primibrachs, proximal interprimibrachs, and anals); however, the stem facet and possibly some fixed brachials exhibited exponential growth in several forms. Blastoids were also mainly characterized by linear development, although a few examples of exponential growth of different parts of a single plate are known (Macurda, 1966).

In most camerates, fixed brachials were added to the calyx throughout ontogeny. Prior to fixation, these functioned as free brachials. Once incorporated, they behaved as calyx elements and their growth was highly integrated and coordinated with adjoining calyx plates.

A growth sequence of internal molds of *Macrostylocrinus cirrifer* shows the relationship between growth of calyx plates and the aboral nervous system. Throughout ontogeny, the grooves housing the nerve cords became wider and deeper as a result of resorption. Accretion of the adjoining calyx plates was arranged so that the previously established aboral nervous system was simply extended. Any other configuration would have resulted in gaps forming between the adjoining calyx plates; clearly, these did not develop. This implies that the aboral nervous system was indirectly responsible for integration and coordination and prevented the formation of gaps. The ultimate control is believed to have been mesenchymal. Not all tegmen plates were in contact with any of the nerve levels. Yet the growth of crinoid tegmens seems to have been highly integrated and coordinated. Probably, the integration and coordination of tegmen growth was completely regulated by the mesenchyme.

In Recent *Antedon,* the ectoneural nervous system first appears in the fourth week of growth (Clark, 1921, p. 485). Although few data are available, this may give rise to the hyponeural nervous system. The aboral nervous system seems to form a little later where it may be determined around the chambered organ during the sixth week (Clark, 1921, p. 499). At any rate, the endoskeleton is well developed and at this time consists of basals, orals, infrabasals, columnals, and radials. Thus, the aboral nervous system develops before the arms. Clearly, the initial growth stages of the above plates which first form about 100 hours after birth cannot be controlled, directly or indirectly, by the aboral nervous system, which does not appear until later. Raup (1966, p. 393) suggested that geometry of echinoderm plates (i.e., shape and position) is controlled by the configuration of the mesenchyme cells which, in turn, is controlled by its physical relation to the overlying epidermis.

This conclusion seems valid for youngest crinoids. In adult Recent crinoids, the ectoderm is poorly developed and consists of a thin syncytial layer, which is almost absent in some forms. The ectoderm is not sharply differentiated from the underlying mesenchyme and the two layers intergrade (Hyman, 1955, p. 48). The ectodermal degeneration of *Antedon* may be traced back to the fifth day and perhaps earlier (Clark, 1921, p. 464, 483). Such degeneration indicates to me that the *Antedon* ectoderm is unable to control skeletal development after early larval growth, although the exact point of no return is not evident. Inasmuch as growth of modern crinoids and the camerates follows the same basic pattern, these findings may be extrapolated to the fossil forms.

Consequently, I conclude that the plate geometry and growth of very young crinoids is determined by the physical relationship of the mesenchyme to the ectoderm. In older crinoids the aboral nervous system may integrate indirectly and coordinate growth of the arms and many calyx plates. The control probably operates through the physical relationship of the aboral nervous system and the surrounding mesenchyme. When the transition from ectodermal control to control by the mesenchyme and aboral nervous system occurs is not known. Possibly the transition occurs before or during appearance of the primibrachs. The embryonic primibrachs *1* of *Antedon* possess an axial nerve cord (i.e., armward extension of aboral nerve cord). Certainly the transition would be expected prior to the

development of secundibrachs. Growth of most tegmen plates is most likely controlled by their relations with the surrounding mesenchyme. The hypothesis is highly tentative. Far more work on the physiology of modern crinoid ontogeny is required before a definitive mechanism can be outlined.

One would expect the brachial ontogeny to be less well integrated and coordinated than that of calyx plates. In most of the latter all margins are in contact with adjoining plates and only the inner and outer sides are not opposed by other plates. The brachial situation is different. Uniserial and biserial brachials possess one or more lateral margins which are free and not bounded by other plates (Fig. 1). The dorsal side is free, whereas the ventral side bears the food groove and covering plates. The following conclusions are based on correlation coefficients (Brower, 1973, p. 315-316). Although the brachial dimensions are less well integrated and coordinated with "size" than calyx plates, the overall ontogeny of brachials is highly correlated with the growth of calyx "size." During ontogeny of the dimensions of the calyx plates, the growth rates generally are large, and high correlation coefficients are observed. On the other hand, growth rates of brachial dimensions with respect to "size" and to other brachial dimensions vary. The largest growth rate of a brachial dimension consists of width where high correlations are seen. Conversely, the small growth rate of minimum height always results in lower correlations. The general trend is for high correlation coefficients to be associated with high growth rates. The development of one brachial dimension vs. another or "size" was commonly exponential. Apparently, this is possible because the brachials are not bounded by adjoining plates on all lateral margins as are calyx plates.

Correlation coefficients are not available for the column ontogeny of camerate crinoids and definitive conclusions cannot be outlined. Probably, the typical integration and coordination pattern is similar to the large brachial dimensions which show high growth rates. The mechanism for brachial and columnal integration and coordination is the same as that for calyx plates.

ONTOGENY OF CALYX PLATES

In Paleozoic crinoids, new calcite was deposited on the margins and exterior surface of calyx plates, no new calcite being added to the inside of plates (Fig. 7,*1-3*). This is evidenced by the locations of growth lines (Brower, 1973, p. 293-294; Lane, 1963a; Meyer, 1965; Macurda, 1968). When present, growth lines are always observed on the interior of calyx plates; this shows that calcite was not deposited on the previously formed parts of the plate interior. Growth lines are not seen on the outsides of crinoid plates. As noted by Lane (1963a), this is related to placement of the aboral nerve cords. These are located along the plate interior, some simply lying on the flat plate surface, others being housed in grooves on the interior of the plate. Deposition of calcite on the plate interior could have interfered with or disrupted the fragile aboral nerve cords. The level of the aboral nerve cord is dominant in crinoids; these nerve cords seem to control posture, e.g., such basic movements as flexing the arms and bending the stem (Moore, 1924). It is critical to note that growth of Paleozoic crinoid plates simply extends the previously established aboral nervous system. These nerve cords do not migrate during ontogeny. In the ray plates that became fixed in the calyx during ontogeny, the internal grooves housing the nerve cords also record the position of the ambulacral tract when these plates were free brachials.

H. B. Moore (1935) showed that growth lines on plate exteriors of living echinoids are seasonal. This cannot be verified for Recent and fossil crinoids, although their growth lines are presumably periodic. In many Paleozoic species these are observed to become more closely spaced toward plate peripheries, which probably denotes slower deposition of calcite in older and larger animals. Some crinoid plates lack growth lines. Comparison with living echinoids (Moore, 1935, fig. 5, 6) suggests that not all growth lines on crinoid plates usually were preserved. Typically, they are not seen on the most immature parts of plates (Wachsmuth & Springer, 1897, pl. 4, fig. 6; Wanner, 1916, pl. 99, fig. 6a,b; Meyer, 1965, fig. 1). Three possible explanations for the complete or partial absence of growth lines are: 1) continuous deposition of calcite throughout

life of the crinoid; 2) obliteration of growth lines by deposition of thin internal calcite laminae, as seen in *Antedon* and Recent echinoids (Moore, 1935), although evidence for this in Paleozoic crinoids is lacking; and 3) nonpreservation of growth lines. Because of the placement of the aboral nerve cords, the first or third of these suggested explanations is preferred.

During the early development of living comatulids such as *Antedon,* the aboral nerve cords lie on the inner sides of the radials (Fig. 7,*4-6*). Subsequent internal deposition of calcite on the plates gradually buries the nerve cords within the theca (Carpenter, 1866, p. 738, 739; 1876, p. 454). Resorption of calyx plates is more common in Recent crinoids than in Paleozoic camerates (Clark, 1915, p. 322-340). In general, plate growth of living forms is far more complex than that of most Paleozoic species.

ONTOGENY OF THE CALYX

INTRODUCTION

In most camerates, free brachials successively became fixed in the calyx throughout growth, although the fixation rate commonly varied with "size" and species. Prior to incorporation, the fixed brachials resembled free brachials. During and immediately after fixation, these plates developed angular margins along which the interbrachials were joined in the calyx. The formation of these angular margins involved relative changes of the various growth rates of width in the new fixed brachials. The fixed pinnulars were joined in the calyx in similar fashion.

The overall degree of integration and coordination of the calyx geometry of camerates was high. Reliable correlation coefficients of the various plate dimensions vs. each other, calyx-plate dimensions vs. "size" and other calyx-shape parameters, and calyx-shape measurements vs. one another range from 0.77 to 0.997; the significance levels of the correlation coefficients almost invariably exceed 0.999. Variation in degrees of freedom makes it difficult to compare the correlation coefficients and their significance levels within a single species and between different taxa. *Alisocrinus tetrarmatus* Brower yields the best data. The ray plates, radials, primibrachs, and proximal secundibrachs were most closely integrated and coordinated with each other and measurements of calyx size. The tertibrach *2,* interprimibrach *1,* primanal, and the basals, all of which are peripheral to the main sequences of ray plates, show lower correlations and significance levels.

The correlations for "size" vs. fixed brachials vary with calyx type. Fixed brachials can be incorporated in the calyx by interprimibrachs and in some cases, also intersecundibrachs, interterti-brachs, etc. The correlations between "size" and the distal fixed brachials are highest when the fixed brachials are joined in the calyx by interprimibrachs; these correlations range from 0.92 to 0.97 and all significance levels exceed 0.999. Where the fixed brachials are incorporated in the calyx by intersecundibrachs and intertertibrachs, a lower degree of integration and coordination is found. These correlation coefficients cover an interval of zero (no fixed brachials added) to 0.92 and the significance levels may be greater than 0.999.

Camerate crinoid calices are divided into five types depending on the extent of fixed brachials, nature of interbrachials, and to some degree on number of arms. The five groups comprise a continuous series. Overlap is common and assignment to a single type may be rather subjective and arbitrary. The five categories are listed as follows:

1. **Xenocrinid.** Many fixed brachials; interbrachials small and irregular; few arms in a ray (Reteocrinidae, Xenocrinidae, some Tanaocrinidae).

2. **Glyptocrinid.** Many fixed brachials; interbrachials large and regular; few arms in a ray (Glyptocrinidae, Scyphocrinitidae, Melocrinitidae, most Archaeocrinidae, some Rhodocrinitidae, Tanaocrinidae, Periechocrinidae, Dimerocrinitidae).

3. **Actinocrinitid.** Many fixed brachials; interbrachials large and regular; numerous arms in a ray (most Actinocrinitidae and Batocrinidae, some Periechocrinidae, a few Rhodocrinitidae).

4. **Patelliocrinid.** Few fixed brachials; interbrachials large and regular; two large primibrachs present in each ray; few arms in a ray

(Gazacrinidae, Desmidocrinidae, Coelocrinidae, Eucalyptocrinitidae, Patelliocrinidae, some Dimerocrinitidae, a few Hapalocrinidae).

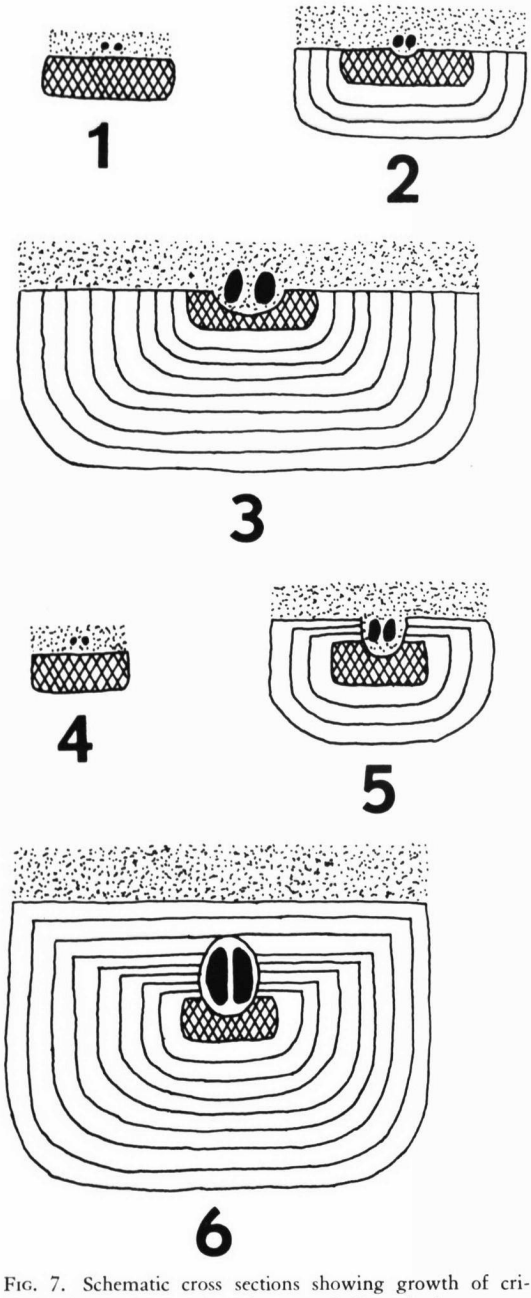

FIG. 7. Schematic cross sections showing growth of crinoid calyx and cup plates by growth lines (soft parts on plate interiors stippled, axial nerve cords black, embryonic plates cross-ruled) (Brower, n).——*1-3*. Camerate crinoid, plates arranged from youngest to oldest.——*4-6*. Recent comatulid, plates arranged from youngest to oldest.

5. **Platycrinitid.** Few fixed brachials; interbrachials few and regular; primibrachs small; one or two in each ray; few to numerous arms in a ray (Nyctocrinidae, Hexacrinitidae, Dichocrinidae, some Hapalocrinidae, Platycrinitidae).

COMPARISON OF GLYPTOCRINID- AND PATELLIOCRINID-TYPE CALICES

Both young patelliocrinids (Fig. 8, 9) and glyptocrinids (Fig. 10, 11) have parts of the primaxil fixed in the calyx. Divergences between the two groups occurred during later ontogeny. All patelliocrinid-type calices examined show an exponential regression line of "size" vs. fixed brachials in the lateral interrays in which the rates of fixed-brachial incorporation declined with increasing "size" and age; the mean range of rates of fixation was smaller than that of glyptocrinid types. Most of the latter crinoids examined are characterized by linear relationships, although a few forms exhibit an exponential pattern.

Another striking difference between the two calyx types is the more extensive formation of intersecundibrachs and intertertibrachs (if more than two arms occur in each ray) in the glyptocrinid group. Young crinoids of both categories have the proximal parts of secundibrach *1* joined together along the ray axis. Some patelliocrinids retained this juvenile configuration (normal crinoids in Fig. 8) but others developed intersecundibrachs and fixed brachials at low fixation rates (Fig. 9). All patelliocrinids studied have only two arms in a ray and intertertibrachs are not observed. The glyptocrinid species formed intersecundibrachs and in some forms intertertibrachs, and the associated fixed brachials at rapid growth rates relative to "size." In crinoids with two arms in each ray (Fig. 11), the intertertibrachs are lacking. Forms with three or four arms to a ray developed these plates and the associated fixed brachials (Fig. 10). Generally, the intertertibrachs were not initiated until after the intersecundibrachs were well under way. Despite the differentials in rates of fixed-brachial development between the two calyx types, the mechanism of brachial and pinnule fixation remained constant.

The variation in rates of fixed-brachial in-

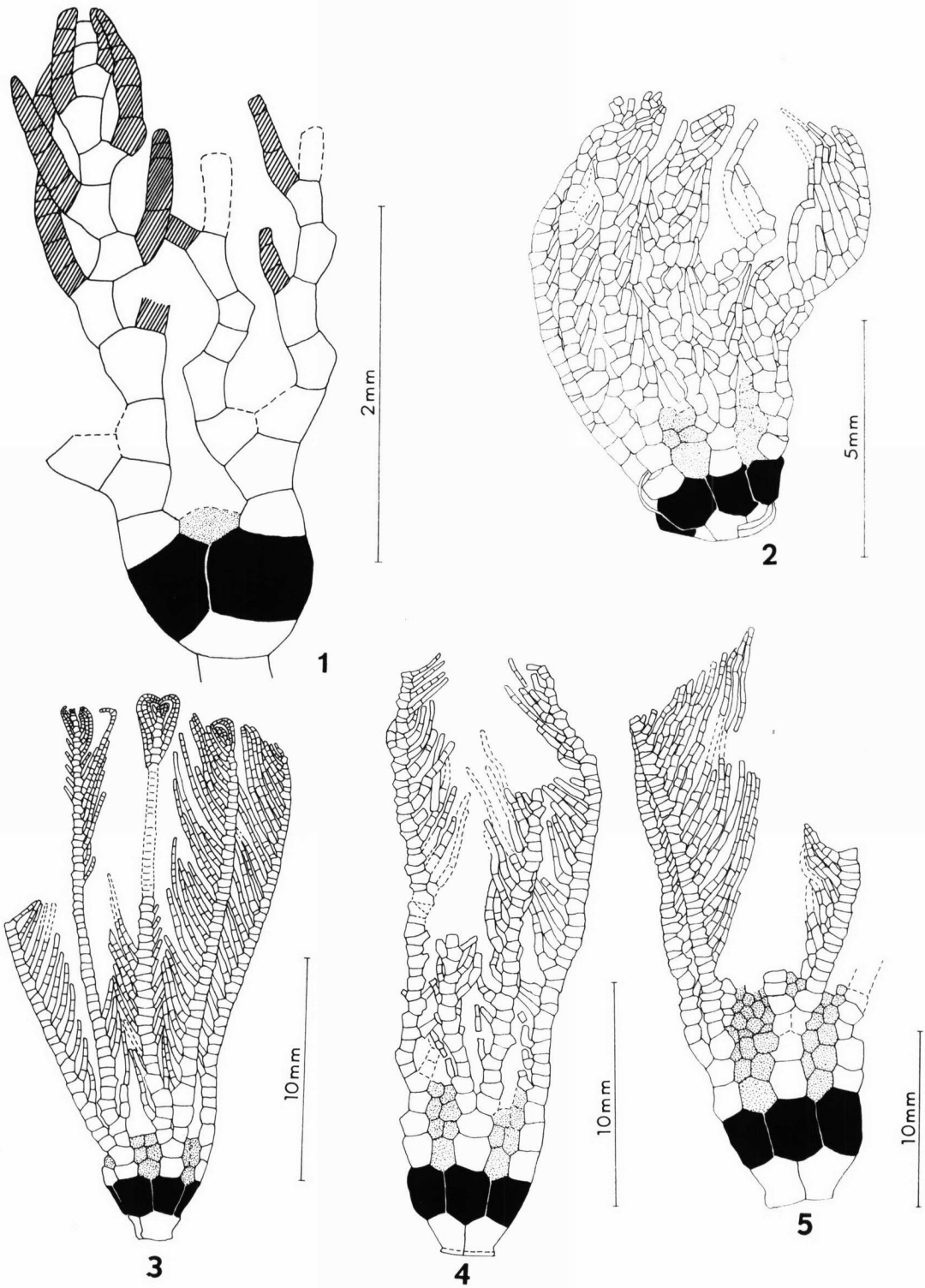

FIG. 8. *(For explanation see facing page.)*

corporation between patelliocrinid- and glyptocrinid-type crinoids caused a series of correlated divergences in growth. Young crinoids which lack intersecundibrachs have closely spaced arms within a single ray and the different rays are separated by wide interray areas. The formation of intersecundibrachs and consequent brachial fixation spread the arms of a single ray apart so these became more widely spaced relative to calyx width; consequently, the interray areas were constricted with respect to "size." If and when the intertertibrachs developed, the arms within a single ray were further spread apart and the adjacent intersecundibrach areas and interray areas were constricted relative to calyx width. Most of this arm spreading was caused by the insertion of the proximal one or two ranges of intersecundibrachs and intertertibrachs; above these levels, the adjacent arms of a single ray tend to come together.

The formation of these intersecundibrachs and intertertibrachs changed the arm distribution around the calyx during ontogeny of glyptocrinid-type calices. In young crinoids the arms of a single ray are closely spaced; the interrays are wide relative to "size." In mature individuals the arms are more evenly spaced around the calyx. This probably prevented the pinnules of adjacent arms from becoming entangled or twisted together. Even arm spacing also enabled each arm to filter a separate water area, which allowed wider and more complete coverage of water surrounding the crinoids. This adaptation was unnecessary for the youngest crinoids, which have short pinnules. Ray spreading of this type is unknown in the patelliocrinids with few fixed brachials. These forms retained the juvenile condition with closely spaced arms in each ray throughout growth because of the low rates of fixed-brachial fixation in the intersecundibrach and intertertibrach areas.

A high rate of fixed-brachial incorporation resulted in rapid distal extension of the calyx and viscera. Thus, given glyptocrinid, and patelliocrinid species with similar proximal calyx shapes, the visceral volume was augmented at a faster rate relative to "size" in the former type.

Intersecundibrachs and intertertibrachs (when present) generally extend higher than the lateral and *CD* interray interprimibrachs in glyptocrinid-type crinoids. Consequently, a strongly lobate tegmen was formed. This configuration is less marked in patelliocrinids.

The formation of numerous fixed brachials may have provided stronger support for the growing arms.

The "size" geometry of the two groups shows a significant difference. Young crowns of both types have similar calices in which radials are the dominant ray plates; primibrachs are subordinate to radials and "size" (young crinoids in Fig. 8-11). Divergence occurred in later development. Mature patelliocrinids more or less retained or accentuated this juvenile arrangement of radials and primibrachs throughout ontogeny. Partly, this was caused by differentials in growth rates: the growth vectors of primibrach height relative to "size" were exceeded by those of the radials. Conversely, glyptocrinid types possessed similar growth rates for radials and primibrachs with respect to "size." This resulted in an adult calyx with primibrachs and radials roughly equal in height and percentage-height contributions to "size."

XENOCRINID-TYPE CALICES

The geometry of a xenocrinid calyx is similar to the glyptocrinid type except for the interbrachials (Fig. 12). In glyptocrinids, these plates are large and regular; probably they were joined rigidly together during life. The xenocrinid interbrachials are small and irregular, closely resembling the tegmens of some flexible and modern crinoids which consist of perisome studded with numerous tiny plates. Presumably, the structures were flexible during life of the crinoid

FIG. 8. Growth sequence of *Eopatelliocrinus scyphogracilis,* a patelliocrinid-type calyx, Upper Ordovician, Girardeau Limestone, Illinois and Missouri (radials black; interbrachials stippled; pinnules oblique-ruled in smallest specimens; crinoids arranged in order of increasing "size") (Brower, 1973).

1. Side view of young specimen with few fixed brachials and one interbrachial in each interray, "size" 1.3 mm.
2. *E*-ray view of juvenile with more numerous fixed brachials and interbrachials, "size" 2.5 mm.
3. Side view of small adult, "size" 4.8 mm.
4. Side view of mature crinoid, "size" 6.6 mm.
5. Side view of largest crown, showing moderately numerous interbrachials and fixed secundibrachs, "size" 9.6 mm.

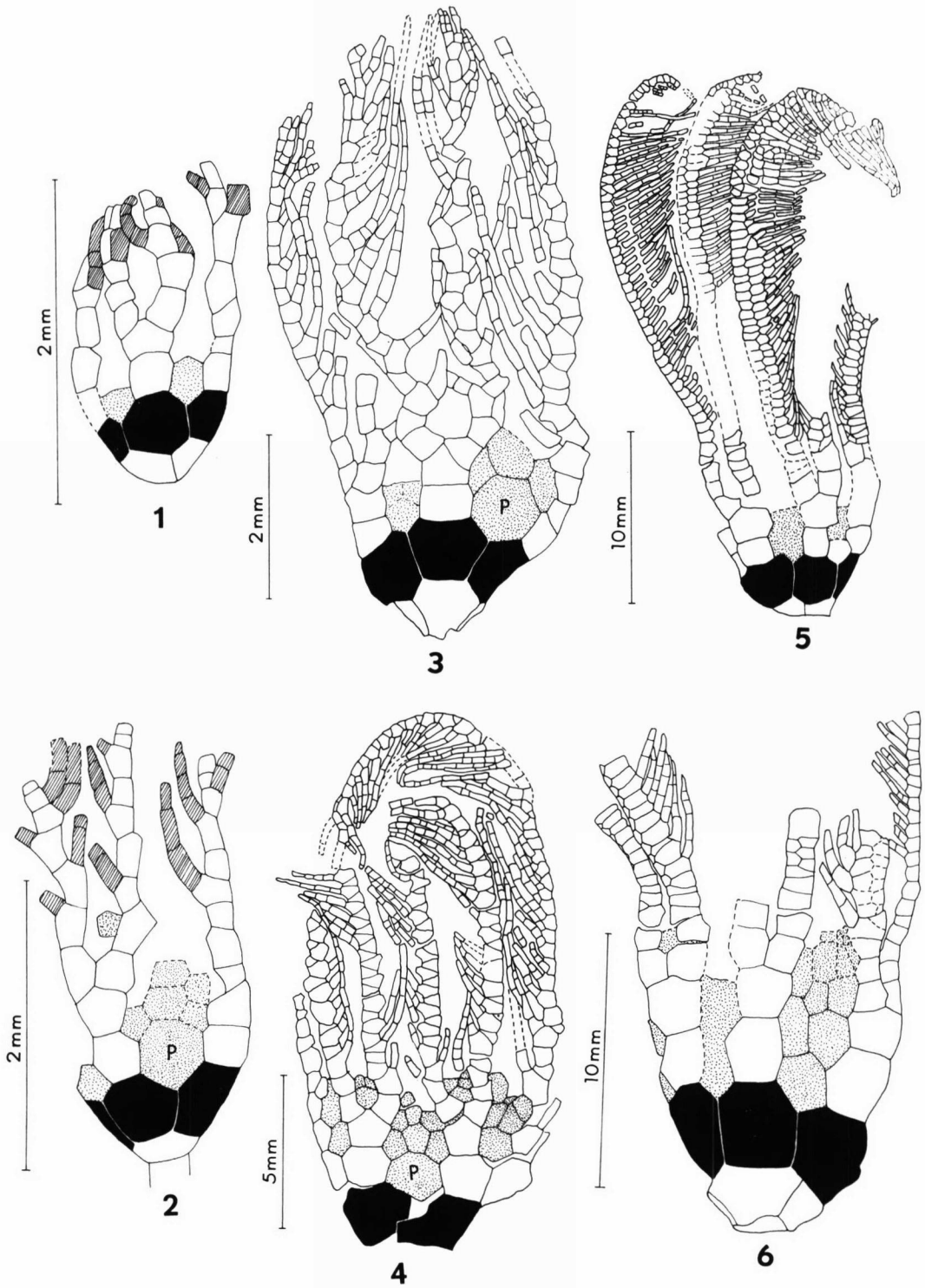

FIG. 9. *(For explanation see facing page.)*

(Brower, 1974). Growth of xenocrinids seems largely to have paralleled the glyptocrinid calyx type except for interbrachials (Brower, 1974). Fixed brachials were incorporated in the calyx of both glyptocrinids and xenocrinids throughout ontogeny by addition of new plates distally. Such plates may have comprised tegmen interambulacrals that shifted downward to become fixed in the calyx. In glyptocrinids, the number of interbrachials at any one level was stabilized after the fixed brachials were incorporated in the calyx. These interbrachials show large growth vectors of height and width relative to "size," whereas the corresponding plates of xenocrinids are characterized by small developmental rates of height and width compared to "size." Consequently, xenocrinid interbrachials remained small throughout ontogeny. In xenocrinids, their areas became wider in larger individuals mainly owing to the intercalation of new interbrachials between older plates. Apparently, this process continued throughout life. For example, youngest specimens of *Xenocrinus multiramus* Ramsbottom (Fig. 12) have only about three interprimibrachs in a lateral interray at the primaxil level. Adult specimens exhibit about six or seven plates in the same position.

Most crinoid specialists considered calices of the xenocrinid type to be primitive (e.g., Moore & Laudon, 1943, p. 76-101). However, Brower (1974) concluded that *Xenocrinus* and *Reteocrinus* were derived from ancestors with large and regular interbrachials. The growth pattern of the xenocrinid interbrachials is unique among camerates, probably representing a specialized adaptation, perhaps in response to respiration.

ACTINOCRINITID-TYPE CALICES

The basic morphological and developmental features of crinoids having actinocrinitid-type calices parallel the more primitive glyptocrinid group with one exception. The glyptocrinids have few arms in a single ray (usually two to four), whereas six or more arms generally occur in rays of actinocrinitid calices. The evolution toward increase in number of arms was general, reaching a maximum of approximately 80 in some species of *Teleiocrinus*. The development of numerous arms and associated axillaries fixed in the calyx tended to spread the arms apart, because the axillaries are roughly pentagonal and expand distally (Fig. 13). The large number of axillary fixed brachials appears to be correlated with fewness of intersecundibrachs, intertertibrachs and higher interbrachs, which are decidedly less well developed than in the more primitive glyptocrinid camerates (compare Fig. 10, 11, 13).

PLATYCRINITID-TYPE CALICES

Camerates with the arms mostly free have fixed brachials only in a short space above the radials. Only one or two interbrachials are present in each interray. They are most similar to and doubtless derived from patelliocrinid-type calices. Primitive groups, such as the Hapalocrinidae, retained two primibrachs. More advanced types (e.g., Platycrinitidae) tended to lose the primibrach *1* and the primaxil (= primibrach *2*) rested directly on the radial. Two main differentials of growth between the platycrinitid- and patelliocrinid-type calices are recognized (Fig. 14). The arms remained free above the fixed-primaxil throughout platycrinitid ontogeny. The patelliocrinids joined fixedbrachials (both primibrachs and secundibrachs) in the calyx throughout development and proximal secundibrachs usually comprised the most distal fixed brachials in mature individuals. Therefore, given platycrinitids and patelliocrinids with identical shapes of the proximal calyx, the calyx volume was augmented more in the latter group relative to "size."

FIG. 9. Growth sequence of *Macrostylocrinus pristinus,* Upper Ordovician, Girardeau Limestone, Illinois and Missouri, with patelliocrinid-type calyx (*P,* primanal; radials black; interbrachials stippled; pinnules of *1* and *2* oblique-ruled; specimens arranged in order of increasing "size") (Brower, 1973).

1. Side view of youngest crinoid with fixed primibrach *1* and uniserial arms, "size" 1.0 mm.
2. *CD*-interray view of slightly older animal, "size" 1.3 mm.
3. D-ray view of young specimen with strongly wedge-shaped uniserial brachials, "size" 2.4 mm.
4. *CD*-interray view of transitional crinoid with arms composed of strongly wedge-shaped uniserial brachials and immature biserial brachials, "size" 4.4 mm.
5. *E*-ray? view of mature specimen with biserial arms, "size" 7.3 mm.
6. Side view of largest crinoid with moderate number of interbrachials and fixed secundibrachs, "size" 10.2 mm.

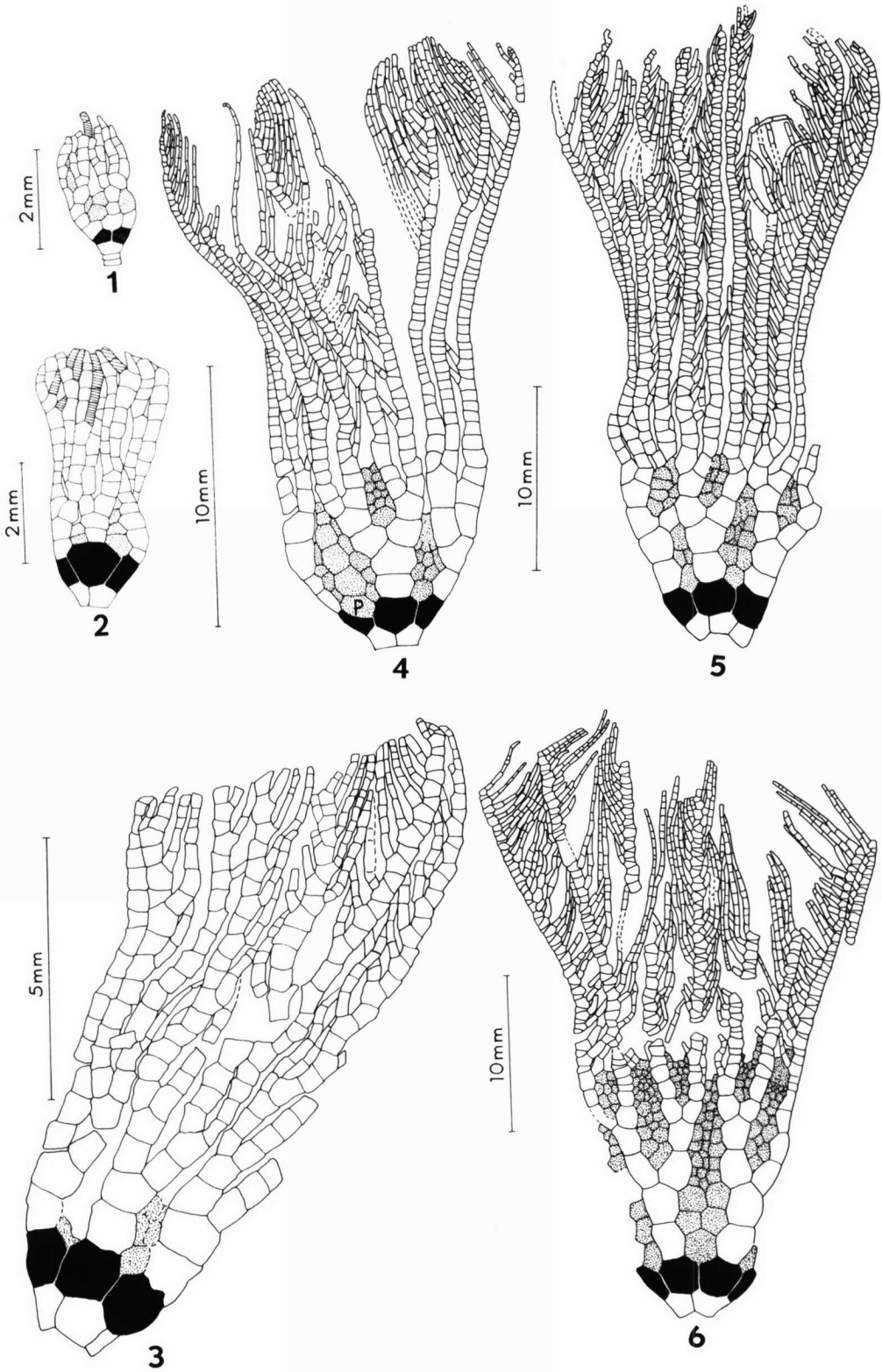

FIG. 10. *(For explanation see facing page.)*

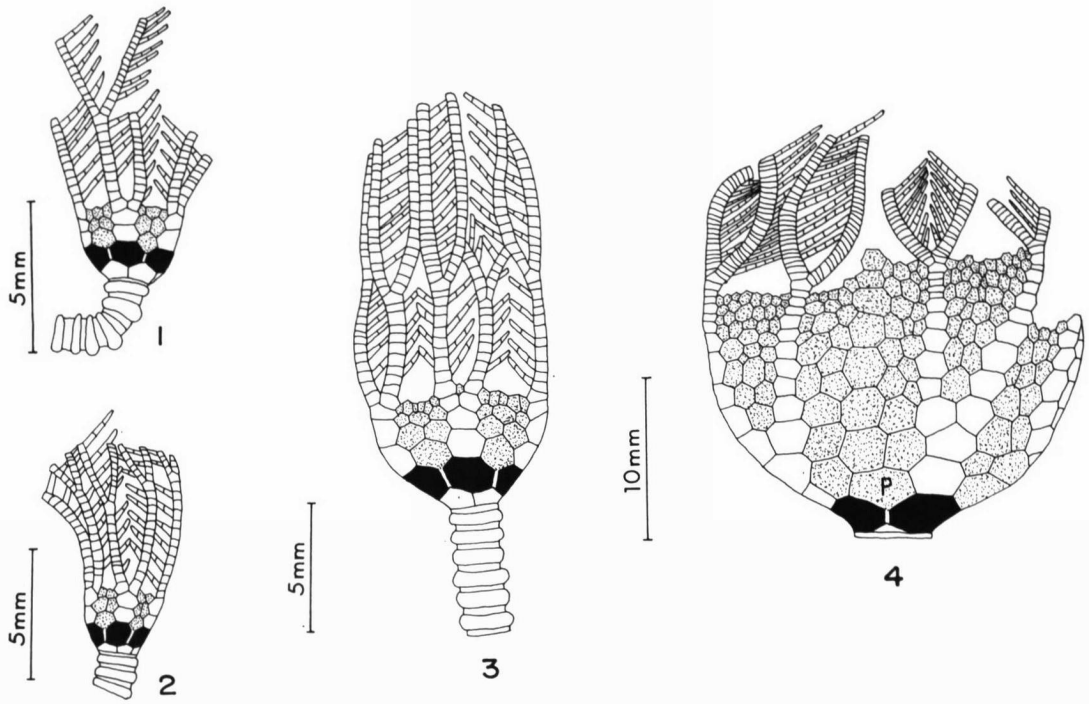

FIG. 11. Growth of *Glyptocrinus dyeri,* Upper Ordovician, Ohio, with glyptocrinid-type calyx (radials, black; *P,* primanal; interbrachials stippled; crinoids arranged from youngest to oldest) (Brower, 1974).

1. Side view of young specimen with few fixed brachials, "size" 2.4 mm.
2. Side view of slightly older specimen, "size" 2.45 mm.
3. Side view of juvenile crown with more numerous interprimibrachs and proximal intersecundibrachs, "size" 3.95 mm.
4. CD-interray view of mature crinoid with many interprimibrachs, intersecundibrachs, and fixed secundibrachs, "size" 9.4 mm.

The width and height growth rates of the primaxil with respect to "size" were much smaller in platycrinitids than in patelliocrinids. Thus, the platycrinitid primaxil became progressively smaller in relation to "size" throughout growth. In young *Platycrinites bozemanensis* (Miller & Gurley) (Fig. 14), a pentagonal primaxil completely supports the secundibrachs *1.* Mature individuals have a triangular primaxil which only partially serves this function; the outer margins of secundibrach *1* rest on the radials. Although advanced crinoids, like *P. bozemanensis,* comprise extreme cases, the growth vectors of primibrachial width and height in these camerates generally were exceeded by those of patelliocrinid-type calices.

FIG. 10. Growth sequence of *Alisocrinus tetrarmatus* with glyptocrinid-type calyx, Upper Ordovician, Girardeau Limestone, Illinois and Missouri (radials, black; interbrachials stippled; pinnules oblique-ruled in *1* and *2*; specimens arranged in order of increasing "size") (Brower, 1973).

1. Side or *CD*-interray view of smallest crinoid showing few fixed brachials and short arms composed of few brachials, "size" 1.1 mm.
2. D-ray view of slightly larger young specimen with better developed arms, "size" 1.8 mm.
3. Side view of juvenile crinoid, "size" 3.4 mm.
4. C-ray view of young adult showing development of proximal intersecundibrachs, "size" 4.2 mm.
5. Side view of submature adult, "size" 6.4 mm.
6. Side view of largest crinoid with numerous interprimibrachs, intersecundibrachs, intertertibrachs, and fixed brachials, "size" 9.0 mm.

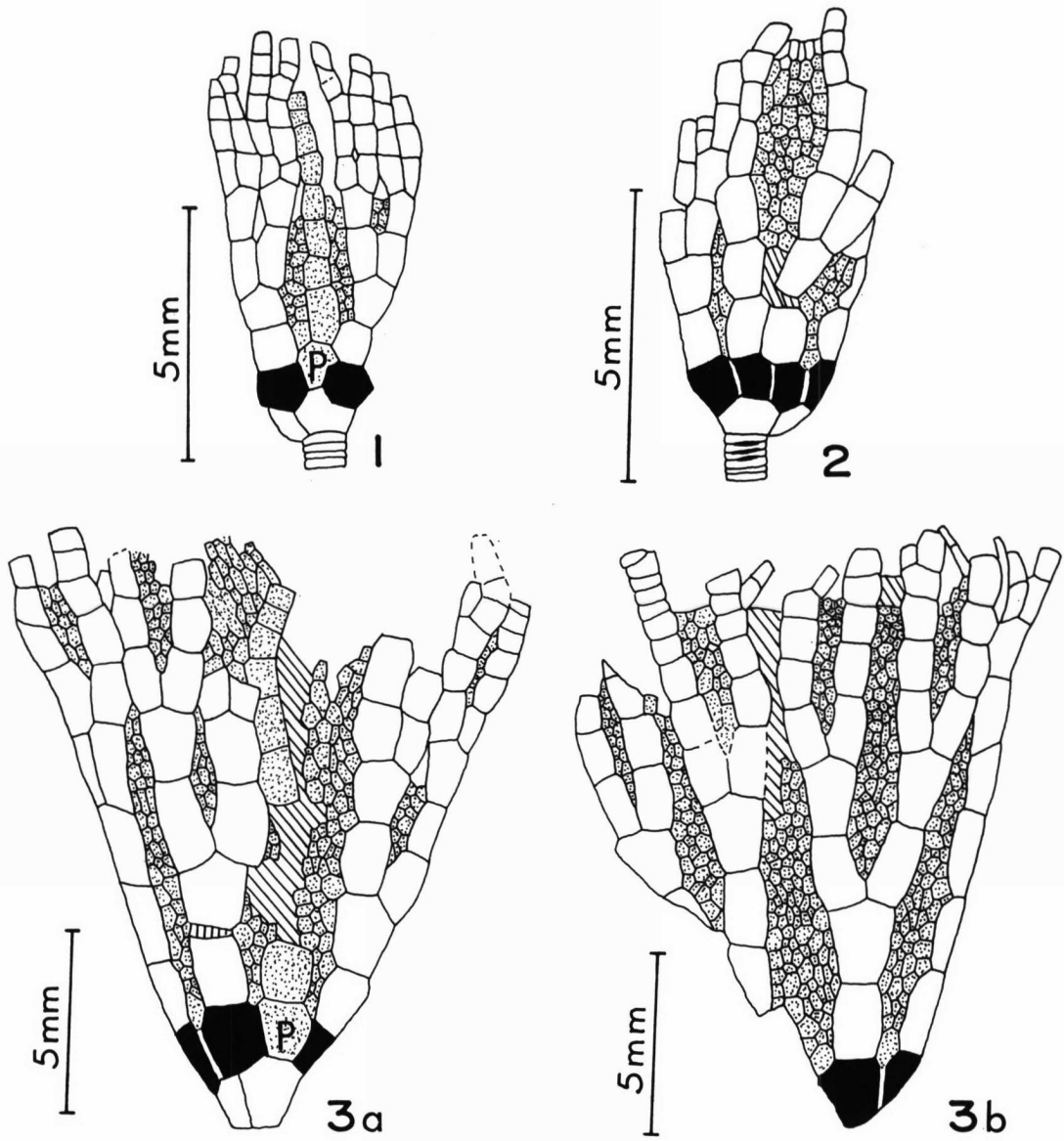

FIG. 12. Growth sequence of *Xenocrinus multiramus,* Upper Ordovician, Scotland, with xenocrinid-type calyx (*P,* primanal; radials, black; interbrachials stippled; damaged parts of specimens oblique-ruled; specimens arranged in order of increasing "size") (Brower, 1974).

1. CD-interray view of young specimen with relatively few interbrachials, "size" 3.2 mm.

2. A-ray view of another young specimen with more interbrachials, the *A*-ray is abnormal and fails to branch, "size" 3.3 mm.

3a,b. CD-interray and *A*-ray views of adult individual with numerous small and irregular interbrachials, "size ranges from 7.5 to 7.8 mm in different rays.

GEOLOGICAL HISTORY OF THE CALYX TYPES IN CAMERATES

It should be emphasized that this is a generalized summary which is designed only to illustrate a large-scale pattern of successions and replacements. Detailed lineages are not delineated and all calyx types were probably polyphyletic. For example, the platycrinitid-type geometry is common in both the Hapalocrinitidae and the Hexacrinitidae. The former group probably had Patelliocrinidae ancestry, whereas the latter was most likely descended from the Desmidocrinidae (Moore & Laudon, 1943, p. 76-101; Brower, 1973, p. 401-407). The general distribution of calyx types in Paleozoic camerates is listed in Table 2. This overall pattern suggests that during the early and middle Paleozoic: 1) xenocrinid-type calices evolved from glyptocrinid types, but, because these were not successful, they were replaced probably by glyptocrinid types (Brower, 1974); 2) extinct glyptocrinid groups were succeeded by actinocrinitid and patelliocrinid types; 3) platycrinitids supplanted patelliocrinids and perhaps some others. After early Mississippian time camerates were characterized by low diversity and were unsuccessful except for a "last stand" in the Permian of Timor; soon after, camerates became extinct. During this late Paleozoic interval, the camerates probably were replaced by inadunates and flexibles, if they were supplanted by crinoids. Inadunates, flexibles and articulates almost exclusively have arms free above the radials and the basic calyx geometry of these crinoids is similar to platycrinitid-type camerates. All Mesozoic and Cenozoic crinoids except the inadunate *Encrinites* are assigned to the Articulata and except in *Uintacrinus* have arms free above the radials. This indicates that crinoids lacking fixed brachials were most successful in the long run.

TABLE 2. *Qualitative Distribution of Paleozoic Camerate Calyx Types.*

[The data are compiled from known diversity (*e.g.*, Moore, 1952) weighted by subjective measures of relative abundance.]

	OVERALL CAMERATE ABUNDANCE AND DIVERSITY	XENOCRINID	GLYPTOCRINID	ACTINOCRINITID	PATELLIOCRINID	PLATYCRINITID
Permian	low	absent	absent	rare	absent	rare
Pennsylvanian	low	absent	absent	absent	absent	rare
Mississippian	highest	absent	subordinate	abundant	subordinate	abundant
Devonian	high	subordinate	common	common	common	common
Silurian	high	subordinate	abundant	common	abundant	common
Ordovician	moderate	common	common	subordinate	subordinate	rare

GROWTH OF THE CAMERATE TEGMEN

The ontogeny of the tegmen of camerate crinoids has not been studied in detail. The presence of growth lines on the interiors of many tegminal plates indicates no inward calcite accretion and the ontogeny of these plates seems to have paralleled that of calyx plates. Some ambulacrals may have undergone deposition of secondary calcite on the plate interiors, although this is uncertain because of problems introduced by preservation. All tegminal plates of camerates exhibit outward and lateral growth increments. Resorption of these plates was either nonexistent or uncommon. The tegminal plates of camerates were not in contact with the aboral nervous

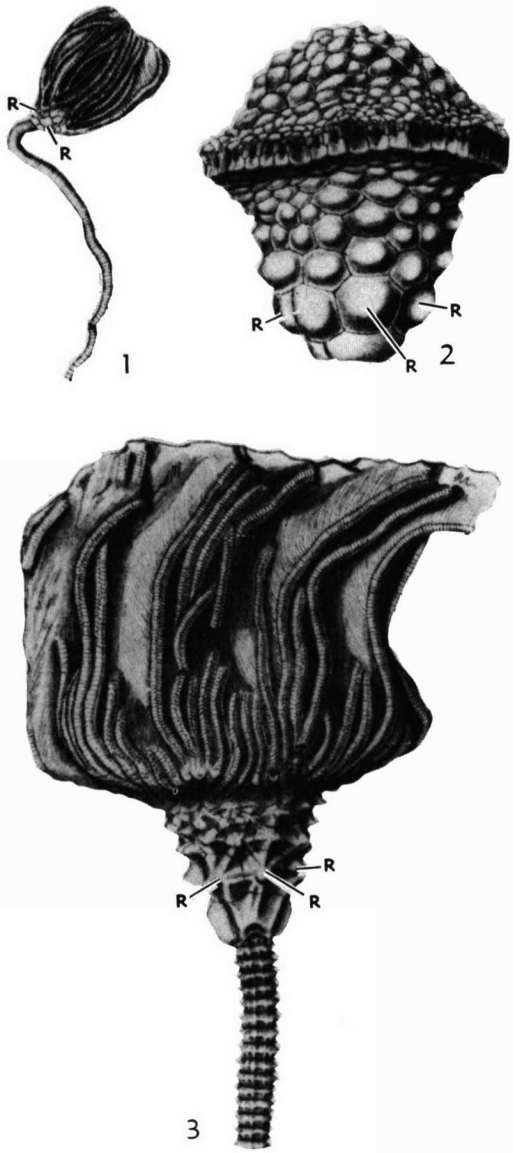

FIG. 13. Growth sequence of *Teleiocrinus umbrosus*, Lower Mississippian, Mid-continent, with actinocrinitid-type calyx (*R*, radial) (Wachsmuth & Springer, 1897). ——*1*. Side view of a young crinoid with arms free above the secundibrachs, ×1.——*2*. *A*-ray view of adult with many fixed brachials and fully developed wheel-like rim of free-arm bases, ×1.——*3*. Side view of submature adult with moderately numerous fixed brachials and incipient wheel-like rim at free-arm bases, ×1.

system; by analogy with Recent crinoids, this passed from the calyx to the free arms (Fig. 4). Some ambulacral interiors of camerates may have been in contact with the hyponeural nervous system (Haugh, 1973, p. 86). The fact that many tegminal plates of camerates were not closely associated with the nervous system suggests that the plate ontogeny was regulated by the mesenchyme.

During ontogeny, new plates were incorporated in the tegmen of most camerates. For example, in *Neoplatycrinites dilatatus* Wanner, the youngest observed individuals have a tegmen composed of five orals and five first axillary ambulacrals with two arm openings in each ray (Wanner, 1937, p. 78, fig. 1-7; Breimer, 1962, p. 137, 138). The largest specimens show six arm openings in a ray and third axillary ambulacrals joined in the tegmen. Aside from the axillary ambulacrals, the tegminal plate structure of these platycrinitids was stabilized. According to Breimer (1962, p. 134-140), the axillary ambulacrals represent highly modified covering plates (see also Wachsmuth & Springer, 1897, p. 103, 104).

In *Glyptocrinus decadactylus* Hall new ambulacrals and interambulacrals were fixed in the tegmen throughout growth (Wachsmuth & Springer, 1897, p. 270, pl. 20, fig. 4a-e). The ambulacrals probably were derived from covering plates of the brachials which were incorporated in the calyx. Origin of the interambulacrals is obscure. I suggest that these were intercalated between older plates along the periphery of the tegmen.

FIG. 14. Growth sequence of *Platycrinites bozemanensis*, Lower Mississippian, Montana, with platycrinitid-type calyx (radials black; interbrachials stippled; crinoids arranged in order of increasing "size") (modified from Laudon, 1967).——*1*. Anterior view of young specimen with relatively large axillary primibrach *1* and uniserial free arms consisting of relatively high brachials.——*2*. Side view of older crown with relatively wider and shorter uniserial brachials.——*3*. Juvenile crown with strongly cuneiform brachials in upper arms.——*4*. Mature specimen with biserial arms, small primaxil and outer edges of secundibrachs *1* resting on radials, proximal part of free arms above axillary secundibrach *2* uniserial but regularly biserial higher.

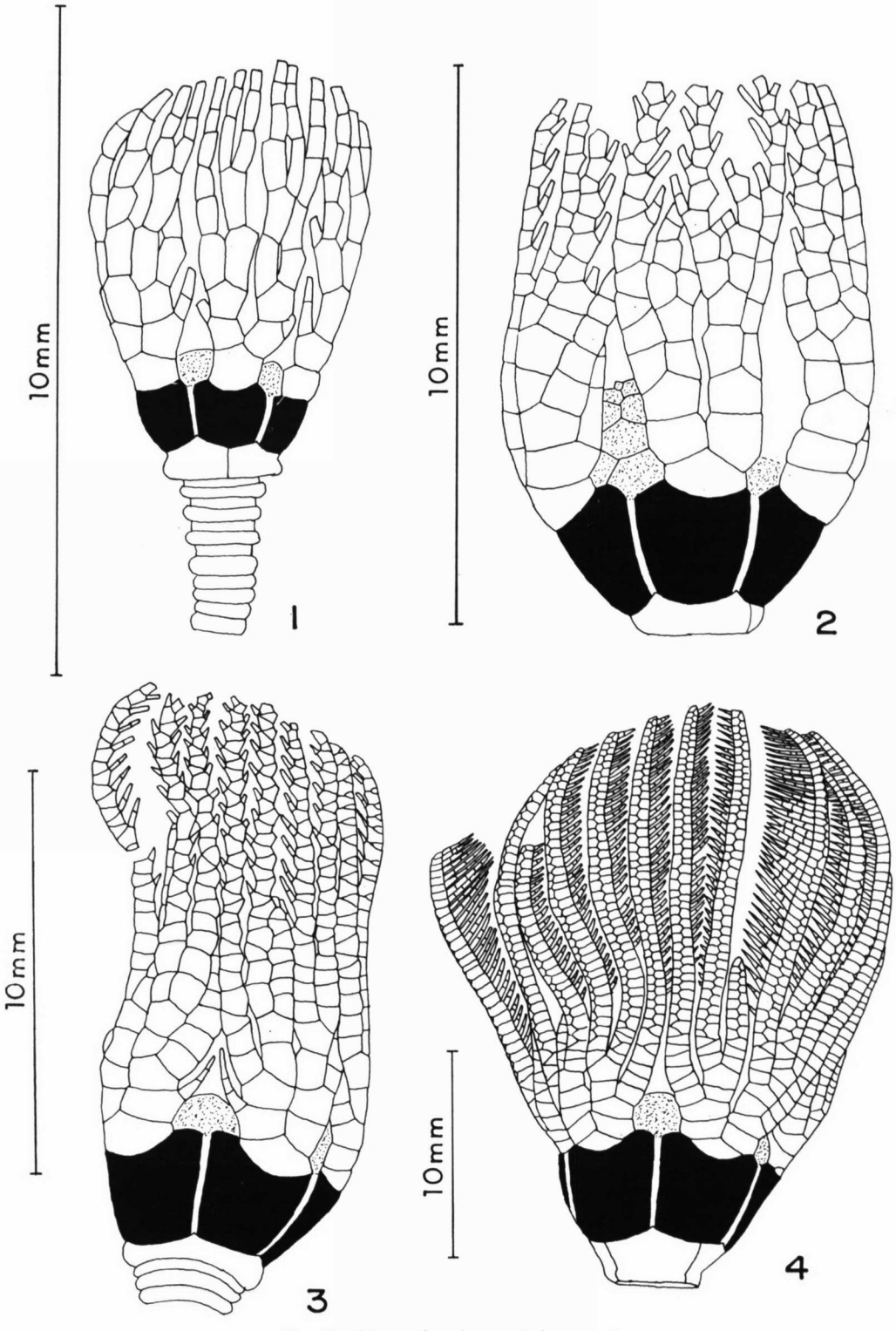

FIG. 14. *(For explanation see facing page.)*

BRACHIAL GROWTH

INTRODUCTION

Development of brachials follows the same pattern seen in the radials of living and fossil crinoids. The radials are the first ray plates formed during ontogeny and they establish the growth pattern of all subsequent ray plates, both fixed and free brachials. The role played by the radials during growth of the rays establishes the paramount importance of these plates in crinoid taxonomy.

Generally, axes of the axial nerve cords constitute constant points of topographic reference. Brachial accretion simply extends these throughout ontogeny. Lateral migration of the nerve cords and resorption of the brachials is either absent or minimized as much as possible. Uniserial pinnulate and nonpinnulate brachials are characterized by gradual incremental growth. This is also true of the uniserial and biserial phases of growth in biserial plates. Biserial brachials underwent major metamorphosis, however, and resorption during the change from uniserial to biserial growth phases.

UNISERIAL NONPINNULATE BRACHIALS AND PINNULARS

All flexible and some inadunate crinoids have uniserial nonpinnulate brachials. The axial nerve cord, food-gathering system, and associated organs were housed in a single V-shaped ventral food groove. By analogy with extant crinoids, the axial nerve cord lay at the base of the ventral groove (Fig. 4; 15,*1,8*). The food groove was deepened by calcite deposition along its ventral margins (Fig. 15,*8*, which depicts the ontogeny of a uniserial pinnulate brachial, nonpinnulate brachials developing in the same way). Calcite accretion also extended the other dimensions. In living and, presumably, fossil crinoids, the diameter of the axial nerve cord increases during ontogeny. This probably caused some resorption along the base and associated sides of the ventral groove. Nevertheless, the axis of the ventral food groove formed a constant point of reference throughout development. The pinnulars of camerate and most inadunate crinoids are also characterized by this growth pattern.

CYATHOCRINITID BRACHIALS

The immature brachials of many cyathocrinitids have the axial nerve cord located at the base of the ventral food groove (Fig. 15,*1*). During growth, the food-gathering structures migrated ventrally and the feeding tissue was eventually separated from the axial nerve cord by calcite deposition. Throughout later ontogeny, the axial canal and nerve cord increased in diameter as a result of calcite resorption along its margins (Fig. 15,*2,3*). However, the axis of the nerve cord comprises a constant point of topographic reference throughout ontogeny.

UNISERIAL BRACHIALS OF CAMERATES

GENERAL PATTERN

All uniserial brachials of the camerate crinoids bear pinnules. The axial nerve cord lies at the base of the ventral food groove (Fig. 5) as in the nonpinnulate brachials of flexibles and some inadunates (Fig. 15,*1*). In ventral view, the food grooves are roughly Y-shaped (Fig. 1; 15,*4-7*). The brachial food grooves are straight and lie at angles to each other, but the food grooves on the pinnule facets are curved. The axis or base of a food groove is located approximately at the center of the structure. As previously mentioned, the food-groove axes constituted constant points of topographic reference throughout life and calcite accretion simply extended these. If resorption occurred, it was confined to the bases of the food grooves and was caused by an increase in diameter of the axial nerve cord in older crinoids. This did not result in movement of the food-groove axes.

Uniserial brachials retained the same basic geometry throughout development, although the height/width ratio and other dimensions varied with age (Fig. 15,*5-7*). All ontogenetic changes were gradual and incremental.

The development of "size" vs. various brachial parameters and combinations of the brachial measurements vs. each other follows either linear patterns with constant growth vectors or exponential regression lines where growth rate changes with age.

The distribution of growth rates indicates that the plan of brachial ontogeny minimized calcite accretion across the articular surfaces as much as possible within basic geometrical limits. Minimizing these vectors causes the least possible interference with ligaments and muscles which hinged and flexed the contiguous brachials. The relative growth rates toward the articular surfaces, listed from greatest to least, are: pinnule facet, distal brachial, and proximal brachial. The

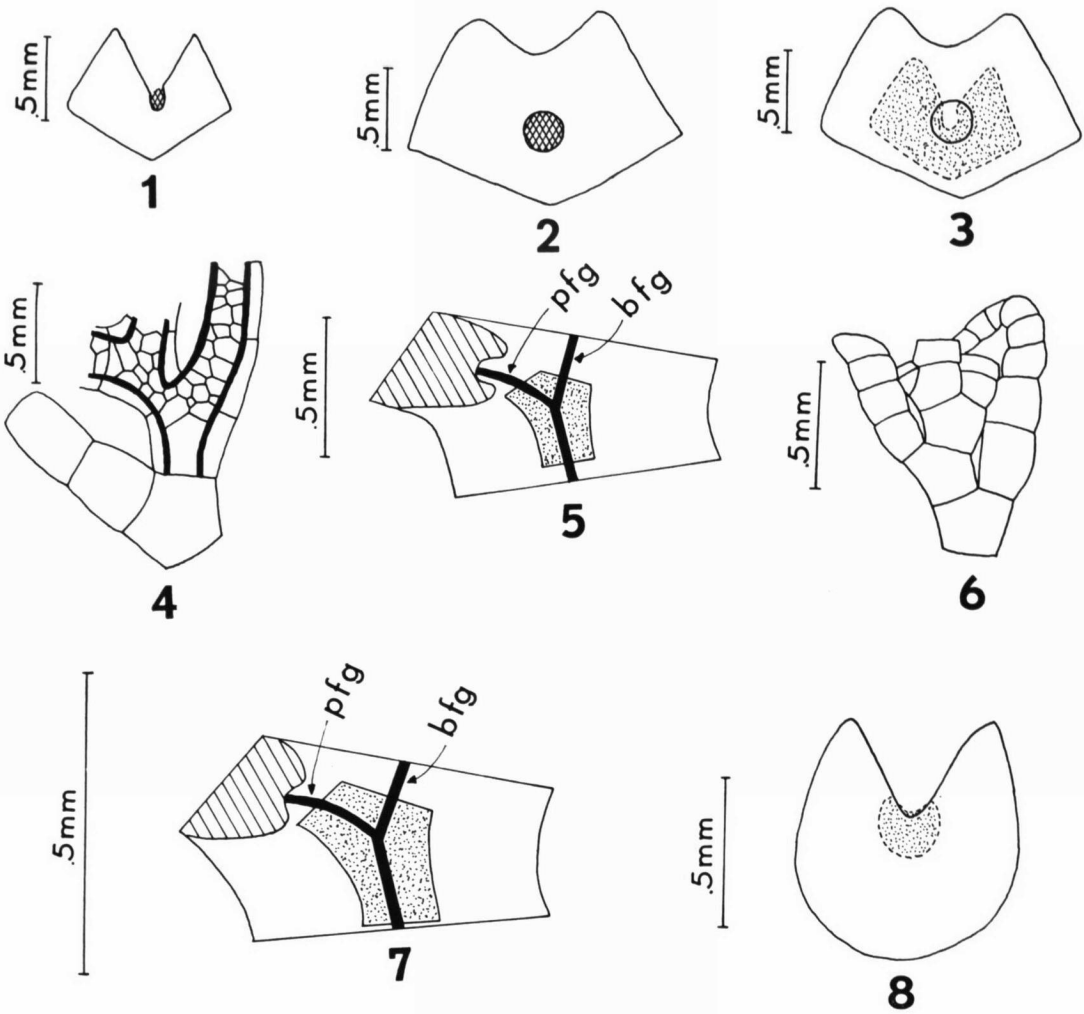

FIG. 15. Growth of uniserial brachials in fossil crinoids (modified from Brower, 1973). [Explanation: axial nerve cords, cross-ruled; food-groove axes, black; *bfg*, brachial food groove; *pfg*, pinnule facet food groove; pinnule facet, oblique-ruled.]

1-3. Nonpinnulate brachials of cyathocrinid *Gissocrinus goniodactylus*, Upper Silurian, Gotland, Sweden, articular surface views.——*1, 2.* Immature and mature brachials.——*3.* Superposed brachials illustrated in *1* and *2*, smaller one stippled and with dashed outline.

4, 7. Uniserial pinnulate brachials of *Eopatelliocrinus latibrachiatus*, Upper Ordovician, Girardeau Limestone, Illinois and Missouri.——*4.* Ventral view of distal arm tip with food grooves outlined in heavy black, covering plates diagrammatic.——*7.* Superposed outlines of two growth stages.

5, 6. Eopatelliocrinus scyphogracilis, Upper Ordovician, Girardeau Limestone, Illinois and Missouri.——*5.* Superposed outlines of two growth stages.——*6.* Dorsal view of distal arm tip.

8. Superposed outlines of two idealized growth stages of pinnulate camerate brachials in articular surface view.

calcite accretion differentials closely correlate with mechanics for support of the developing arms. The rapidly developing vectors of width provided increased supporting area for the growing arms and pinnules. The lowest accretion vector (proximal height) was directed toward the facet which supports the higher brachials. The largest growth rate of an articular surface was toward the pinnule facet which holds only a corresponding pinnule.

The immature brachials present a comparatively high and angular appearance with prominent pinnule facets that are roughly horizontal. Mature plates are relatively wider and possess smoother outlines with less prominent and more steeply inclined pinnule facets than juvenile brachials. This growth trend was caused by the large developmental vectors of width relative to those of height and the change in inclination of the pinnule facets.

The convergence angle between proximal and distal faces of brachials decreased throughout ontogeny. Usually, the angle drops most rapidly in the youngest brachials and more slowly in mature plates. Smaller convergence angles are due to changes in the growth rates of maximum and minimum height relative to each other and the large accretion vectors of width with respect to those of height.

In young crinoids and juvenile brachials of adults (near distal arm tips), the height axes of succeeding plates are not parallel, imparting a crooked or bent appearance to the arms (Fig. 15,*6*; young crinoids in Fig. 8, 10). This configuration is produced by unequal angular convergence of the proximal and distal brachial faces. The convergence angle of the distal face exceeds that of the proximal one. Owing to alternation of the pinnules from one side of an arm to the other, the length axis of the arm remains straight. During later growth, the height axes became more or less parallel because equal or nearly equal convergence angles of the proximal and distal faces of the brachials are formed by adjustments in the various growth rates of height (compare mature and immature crinoids in Fig. 8, 10; mature and immature brachials in Fig. 15,*5,7*).

Ontogenetic changes in the inclination angles of the brachials and in the pinnule facets dictate corresponding changes in the pattern of the food-gathering system. The pinnules of young crinoids are relatively wide-spaced and offset with respect to one another. Probably these offset pinnules filtered a larger area of water than if they were not offset. However, the adjacent pinnules are separated by wide gaps and the water in the immediate vicinity of the arms was probably not completely filtered. In mature plates, after additional brachials developed at the arm tips, support became critical and the height axes of the brachials grew nearly parallel to one another, thus providing more stable support (compare mature and immature crinoids in Fig. 8 and 10). The adjacent pinnules of adult brachials are close-spaced and the food-gathering system of mature animals probably filtered the water almost completely where the arms extend.

On the ventral side rates of calcite accretion probably were small or nil at the axes of the food grooves (Fig. 15,*8*). Deepening of the food grooves was produced principally by deposition of calcite on the ventral areas flanking the food grooves. Some resorption probably occurred along the base and sides of the food grooves, resulting in increased diameter of the axial nerve cords. The dorsal developmental vectors probably exceeded the ventral ones.

REGULATION OF UNISERIAL BRACHIAL GROWTH

The correlation coefficients for the brachials are obtained from "size" vs. brachial dimensions and various brachial parameters vs. each other. The correlations and their significance levels are directly proportional to the growth rate of the brachial dimension involved. Higher correlations are associated with the largest growth rates, namely, those of width and maximum height, while minimum height and size of the pinnule facet show lower correlations. Slightly lower correlation coefficients are observed when the brachial dimensions are correlated with "size" than when the brachial dimensions are correlated with each other. This shows that the brachial ontogeny is less well integrated and coordinated with the development of calyx size than with that of the adjacent brachials and brachial dimensions. The significance levels of the correlation coefficients vary greatly and these may range from above 0.999 to less than 0.900 in any one form. However, considering the low growth rates of the brachial parameters with respect to "size"

and each other, the brachials exhibit highly correlated development.

DISTAL TIPS OF UNISERIAL ARMS

As in living crinoids, camerates formed new brachials throughout ontogeny, although the rates of brachial addition varied with age and species. All new plates developed at the distal arm tips.

The distal tips of the arms bear one or, rarely, two uniserial brachials that lack pinnules. These terminal brachials exhibit parallel proximal and distal faces. The least mature ones have rounded distal margins but slightly older terminal plates are characterized by angular distal margins (Fig. 8; 10; 15,*6*). The highest pinnulate brachials occur immediately below the terminal brachials. Small pinnule facets are present with a short pinnule consisting of one or two pinnulars. The proximal and distal faces converge on each other. Apparently the maximum and minimum heights became differentiated as soon as the pinnule facet and its pinnule appear.

BRACHIALS OF MODERN CRINOIDS

All Recent crinoids are characterized by uniserial pinnulate brachials. The only growth sequence examined is that of *Metacrinus* sp. (Fig. 16). The overall shape of these plates is reasonably similar to the uniserial brachials of camerates. In most immature plates, the axial nerve cord and food-gathering apparatus lie in a single ventral groove. During later growth, the food-gathering tissue is displaced ventrally by calcite deposition. Eventually, the axial nerve cords are fully separated from the food-gathering tissue, and the axial nerve cords are housed within the brachial as in cyathocrinitids mentioned earlier.

The main axial nerve cord is straight and extends from the proximal to distal face of the brachial (Fig. 16,*1*). The diameter of this nerve cord increases throughout ontogeny owing to resorption along its margins, but its axis remains in the same place throughout ontogeny. The main axial nerve cord gives rise to branches that run toward the pinnule facet. The two inner ones are the proximal and distal inner branches. The distal inner branch migrates distally and toward the pinnule facet through calcite resorption and redeposition while expanding owing to resorption along its margins. The proximal inner branch increases in diameter but it does not migrate on the brachial. Closer to the pinnule facet, the proximal and distal branches join and form a single nerve cord. At the pinnule facet, this bifurcates, with each branch emerging on opposite sides of the transverse ridge. Obviously, this is related to the presence of a transverse ridge on the pinnule facet. During growth, the unbranched part of the nerve cord is extended toward the pinnule facet along a line midway between the two nerve-cord branches of the pinnule facet. The branches of the pinnule facet migrate outward toward the pinnule facet as a result of lateral resorption and redeposition. The proximal inner branch, the unbranched part and the mean position of the two nerve-cord branches on the pinnule facet form constant reference points for the growth of a single brachial (Fig. 16,*1-6*). Thus, growth extends the most important elements of the nervous system that was previously established. The food-groove axes roughly overlie the main axial nerve cord and the mean position of its branches to the pinnule facets. The parallelism is not exact, however, and the food-groove axes do not form constant points of topographic reference throughout ontogeny. The food-groove configuration is similar to that of a uniserial camerate brachial.

Axillary ontogeny (Fig. 16,*7-9*) follows the same pattern except that pinnules, pinnule facets, and their associated nerve cords are lacking. Rather, the main axial nerve cord bifurcates near the base of the axillary with one branch continuing on to each of the next brachials. These axial nerve cords are widened due to resorption but they do not migrate laterally within the axillary.

To summarize, the ontogeny of the axial nerve cords of modern crinoids parallels that of many cyathocrinitids. The homologies of the various nerve cords have been discussed by Brower (1973, p. 294-298). The development of the major dimensions of brachials in Recent crinoids closely resembles that of uniserial brachials in camerates.

BISERIAL BRACHIALS

Growth of biserial brachials has been studied only in two species, the Ordovician camerate *Macrostylocrinus pristinus* Brower (1973, p. 371-396) and the Carboniferous inadunate *Woodo-*

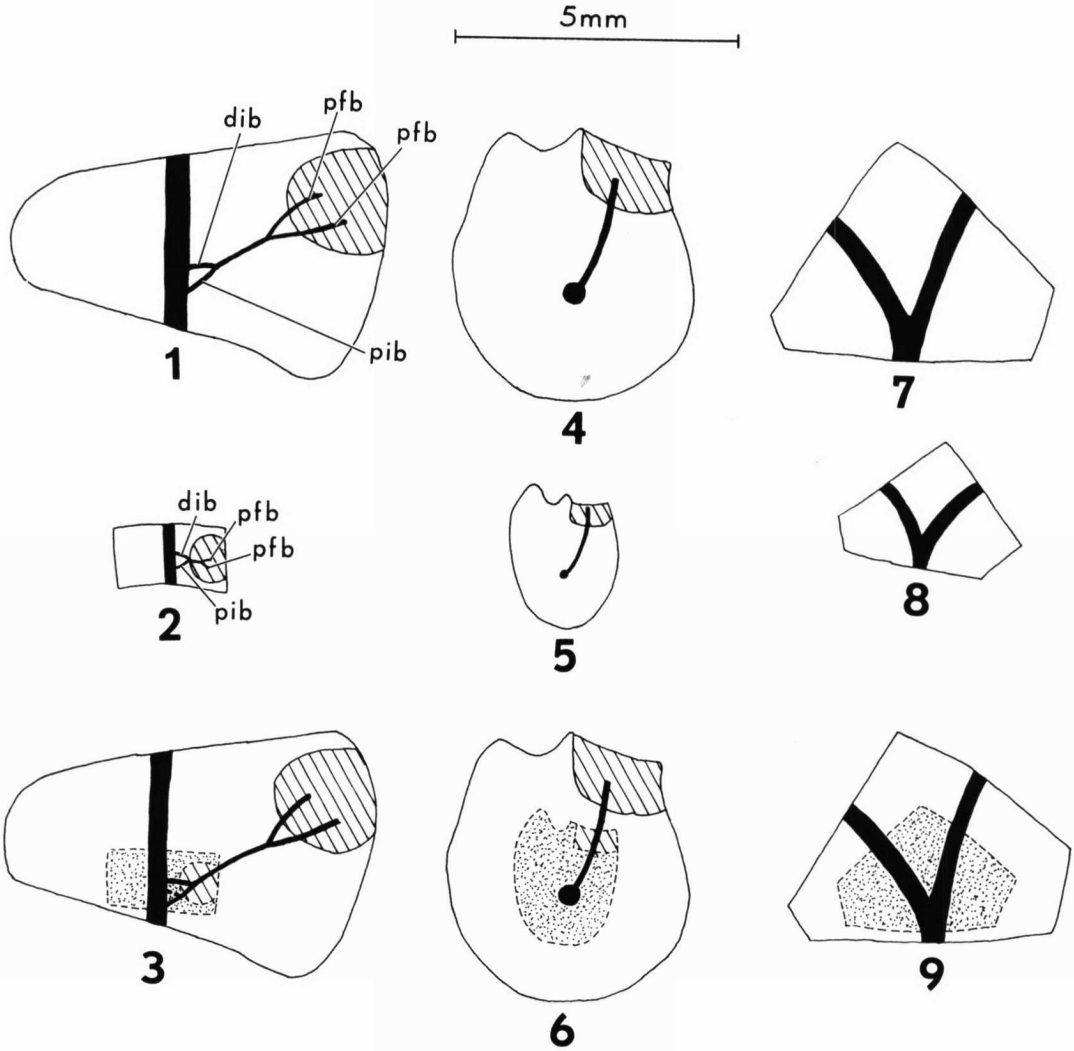

FIG. 16. Growth of uniserial pinnulate brachials of *Metacrinus* sp., Recent (axial nerve cords, heavy black lines; pinnule facets, oblique-ruled) (modified from Brower, 1973).

1, 2. Ventral views of mature and immature brachials (*dib,* distal inner branch of main axial nerve cord; *pib,* proximal inner branch of axial nerve cord; *pfb,* pinnule facet branch of axial nerve cord).
3. Superposed brachials shown in *1* and *2*.
4, 5. Articular surface views of mature and immature plates.
6. Superposed brachials shown in *4* and *5*.
7, 8. Ventral views of mature and immature axillaries.
9. Superposed brachials shown in *7* and *8*.

crinus gravis Wright. The food-groove configurations of crinoids with biserial arms resemble those of uniserial forms except that the food groove of the pinnule facet is straight, rather than curved as in uniserial brachials. The most complete growth sequence is that of the camerate, which is annotated first. To facilitate description, biserial brachial development is divided into the following five phases.

1) During an early uniserial stage, growth paralleled that of a uniserial-armed species in which the ontogenetic vector of the pinnule facet exceeded that of minimum height (Fig. 17,*1-4*). The proximal and distal convergence angles of the brachial faces always increased, unlike the invariable decrease observed in crinoids with uniserial arms. This is related to two different growth rates. Uniserial-armed forms possessed

large growth vectors of brachial width relative to "size" and maximum height, whereas the reverse characterizes biserial brachials. The early developmental rates of minimum height with respect to "size," brachial width, and maximum height were large in uniserial species but small in biserial-armed crinoids. These differentials constitute the first major cause of the divergence of biserial brachials from the uniserial type.

2) The late uniserial stage was a continuation of the previous one except that minimum height began to decrease (Fig. 17,*5,6*).

3) The brachials underwent major changes during a transitional uniserial to immature biserial stage (Fig. 17,*7-9*). The minimum height continued to decrease, so that eventually the inner margins joined and minimum height was nil when the first immature biserial brachials formed. The immature biserial plates have wedge-shapes with curved proximal and distal faces. The inner margins were not yet differentiated from the proximal and distal ones, although the inner area of the plate was in contact with two brachials on the opposite side of the arm (see arms in Fig. 9). Development of the immature biserial brachial involved resorption of the inner sides (opposite the pinnule facet) and the associated proximal and distal faces. This resorption did not affect the food-groove axes of the brachials, although resorption caused most of the increase in the convergence angle. The resorption was dictated by the relations between growth patterns of the brachial width and maximum and minimum heights. The pinnule facets became more steeply inclined, which required lateral migration and probably major resorption of the food-groove axis on the pinnule facet. This axis migration is the second factor which caused the ontogeny of biserial brachials to diverge from the uniserial type.

4) During the change from immature to mature biserial brachials, resorption continued on the inner side of each arm component, thus increasing the convergence angle (Fig. 17,*10,11*). Width growth was asymmetrical, all accretion being directed toward the pinnule facet. Most of the plate exhibits some height growth. The inner margins became strongly differentiated from the proximal and distal ones. Lateral migration of the food-groove axis on the pinnule facet finally ended and growth simply extended the axis established in the previous stage.

5) Within the mature biserial phase, resorption ceased and growth became adjusted so that the brachial faces remained parallel to one another or nearly so (Fig. 17,*12,13*). Although width accretion occurred both toward and away from the pinnule facets, the former growth rate

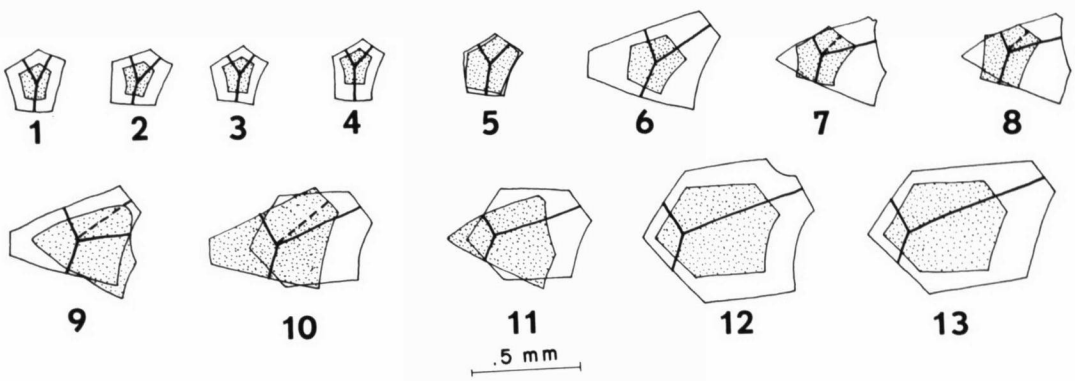

FIG. 17. Ventral-view outlines of biserial brachials in free arms of *Macrostylocrinus pristinus*, Upper Ordovician, Girardeau Limestone, Illinois and Missouri (food-groove axes in heavy black, smaller brachial stippled, if resorption and migration of the pinnule facet food groove was involved, that of the smaller brachial is shown in dashed line) (Brower, 1973).

1-4. Early uniserial stages.
5, 6. Late uniserial stages.
7-9. Transitional uniserial to immature biserial stages.
10, 11. Immature to mature biserial stages.
12, 13. Mature biserial stages.

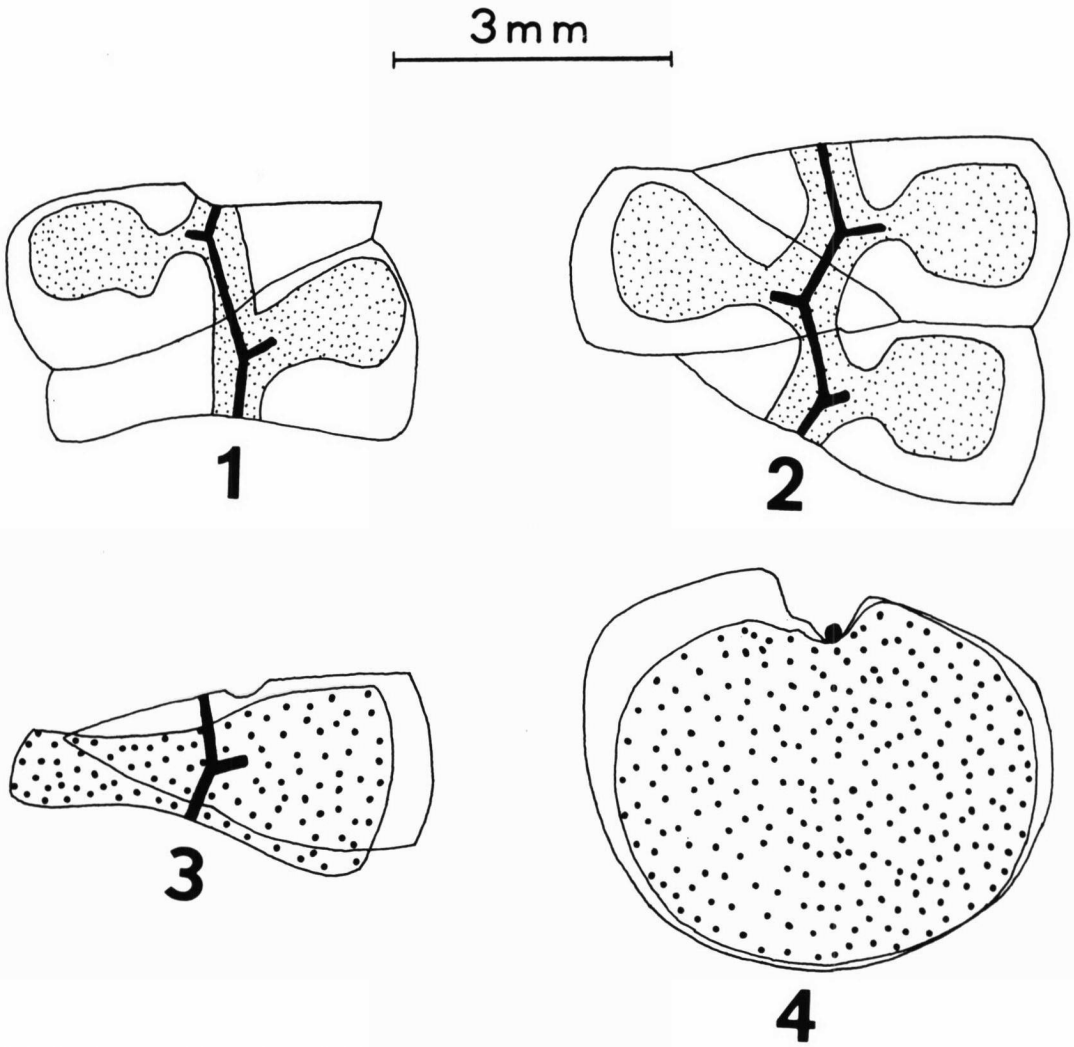

FIG. 18. Growth of biserial brachials in *Woodocrinus gravis,* Lower Carboniferous, Scotland (axial nerve cords, heavy black lines) (Brower, n).——*1, 2.* Ventral views of late uniserial brachials and immature biserial brachials (food grooves and pinnule facets stippled).——*3, 4.* Superposed late uniserial and immature biserial brachials in ventral and articular surface views (late uniserial brachial stippled).

exceeded the latter. Probably, this resulted in minimum interference with the various food grooves and their axial nerve cords. The convergence angle between the inner margins either remained constant or increased, depending on the species.

Woodocrinus gravis Wright shows the transition between the uniserial and immature biserial brachials (Fig. 18). As in *Macrostylocrinus pristinus,* the inner sides of the brachials underwent major resorption. The axes of the axial nerve cords did not migrate on the brachials, however, and growth simply extended them throughout ontogeny. In this respect, development of the inadunate *Woodocrinus* was simpler than in the camerate.

Turning to integration and coordination, the main difference between uniserial and biserial forms consists of the correlation coefficients involving minimum height. In biserial species, these vary from – 0.79 to – 0.92 with significance levels around 0.999. The minimum height correlations of uniserial-armed crinoids are lower and significance levels of less than 0.900 are not un-

common. Thus, minimum height is better integrated and coordinated with the development of "size" and the adjacent brachial dimensions in the biserial-armed taxa than in uniserial-armed forms.

COMPARISON OF UNISERIAL AND BISERIAL BRACHIALS

The nonresorption development of uniserial-type brachials is relatively simple and straightforward. Conversely, resorption is a major factor in the development of biserial brachials. Consequently, in this type, ontogeny is more complex and a higher degree of integration and coordination of the various dimensions is required to prevent gaps from developing between adjacent wedge-shaped brachials. In many crinoids pinnules are more densely packed along biserial arms than uniserial ones, owing to the presence of two rows of pinnulate brachials which alternate from side to side of the arm. Thus, given uniserial and biserial individuals with comparable arm lengths and brachial heights, biserial crinoids possess roughly twice as many pinnules. The amount of curvature observed in many arm segments indicates that biserial arms are more flexible than uniserial arms, at least in species with ill-developed articulations between the brachials.

In Paleozoic camerates and pinnulate inadunates, the usual evolutionary sequence was from uniserial to biserial arms. The ubiquity of this trend shows that it was strongly adaptive to most forms. Virtually all Paleozoic pinnulate crinoids lacked muscular articulations within the arms for most had strictly ligamental articulations. In camerates, distinct transverse ridges generally are not present, although these occur in many inadunates. Usually the ligaments were short and the arms relatively rigid and little flexible. Some late Paleozoic inadunates developed muscular articulations in proximal portions of the arms, although distal brachials retained the ligamental type.

All modern species have recti- or obliqui-uniserial pinnulate brachials with well-developed muscular articulations which allow much flexibility. Apparently, natural selection places a premium on uniserial arms in living forms. Thus, the present selection pressure is reversed from that which prevailed throughout the Paleozoic.

The adaptive significance of the change from uniserial to biserial arms is twofold: 1) development of moderate flexibility which augments arm leverage; 2) increase in number of pinnules in unit arm lengths. The biserial arm has a larger food-gathering system than the uniserial type, for it provides additional food-catching tube feet and a greater area of water coverage, as well as higher arm leverage resulting from increase in arm and pinnule surface areas. In Paleozoic crinoids, these advantages generally prevailed over the disadvantages of the more complex ontogeny of biserial brachials.

In modern species, much arm flexibility is achieved by muscular articulations between the brachials. The adaptive significance of the increased pinnule number in a biserial arm may be less in extant taxa than in Paleozoic forms, because viscera volume relative to arm length seems less in typical living crinoids than in typical Paleozoic ones. Here, the potential advantages of biserial over uniserial arms may be outweighed by the disadvantages of the more complex growth mechanism of biserial brachials. Also, it is difficult to visualize the development of muscular articulations of the modern crinoid type in biserial brachials. In the long run, uniserial pinnulate brachials have proved to be more successful than biserial ones.

ONTOGENY OF THE FOOD-GATHERING SYSTEM

INTRODUCTION

To investigate the ontogeny of the food-gathering system in a crinoid, one wishes to examine such variables as volume of tissue which must be supplied with food and its metabolic rates, number of tube feet that serve in food-catching, area of water covered by the food-gathering system, amount of time spent in feeding, and other factors. Because these variables cannot be measured directly, they can only be approximated by related morphological characters. The quantitative part of this discussion is based on my studies of six camerates from the

Ordovician Girardeau Limestone. All statistics have been recalculated using simple power functions and a slightly revised procedure for equation-fitting; accordingly, the results differ somewhat from data previously published (Brower, 1973). All of the Girardeau crinoids have normal pinnulate arms. Qualitative observations are available on forms with hypertrophied arms or ray trunks.

The investigated variables are the following: 1) "size"; 2) the total volume of tissue is approximated by external volume of the calyx since total amount of tissue cannot be determined because of complex geometry of the crown and unknown complete stems. Both the entire tissue volume and calyx volume are (linear dimension)^3 functions and should scale similarly during ontogeny; 3) length of the entire food-gathering system including the arms and pinnules, which is substituted for the area of water covered by the food-gathering system because it is impractical to measure the area due to its geometrical complexity; 4) number of food-catching tube feet estimated for *Alisocrinus tetrarmatus*; 5) number of free brachials in a single half-ray; 6) length of average pinnule; and 7) length of the free arm or arms in a half-ray.

The functional problem is the usual one that faces filter-feeding marine invertebrates. The food-gathering capacity is, at best, an area or (linear dimension)^2 function, but the tissue to be supplied with food is a volume or (linear dimension)^3 function. The following discussion mainly emphasizes the common solutions to this problem shown by camerate crinoids.

The basic statistics derive from the simple power function or allometric equation $Y = b \cdot X^k$ (see Huxley, 1932, and Gould, 1966, for derivation and discussion of the equation), in which X and Y are the independent and dependent variables, respectively. The intercept b gives the value of Y when X equals unity. Interpretation of b has been subject to much debate as to its biological significance. Here, b is only visualized descriptively as a location and scale parameter for the curve. The exponent k is the ratio of the specific growth rates of Y and X. If k exceeds 1, then Y grows more rapidly than X and the Y/X ratio is augmented with increasing X values (positive allometry). For negative allometry, k is less than 1 and Y/X decreases as X becomes larger. In isometric development, k equals 1, Y/X remains constant, and the Y growth rates per unit increments of X are also stabilized. Under positive allometry, these developmental vectors rise exponentially throughout ontogeny, whereas the reverse characterizes negative allometry.

"Ideal" cases may be defined for the development of various combinations of linear dimensions, areas which are (linear dimension)^2 functions, and volumes or masses which are (linear dimension)^3 functions. "Ideal" should be translated as Y and the variables contributing to Y are direct functions of X. The following "ideals" are treated here: 1) Y and X = two linear dimensions, $k = 1$; 2) Y = an area and X = a linear dimension, $k = 2$; 3) X = a linear dimension, Y = a volume, $k = 3$; 4) X = a volume, Y = a linear dimension, $k = 0.33$; 5) X = a volume, Y = an area, $k = 0.67$. These ideal cases provide scales for comparison with observed k values. For example, if the observed k exceeds ideal k, then Y grows more rapidly and the Y/X ratio increases faster with progressive ontogeny than expected. The opposite situation is seen when the observed value is smaller than the predicted one.

The amount of integration and coordination seen during ontogeny is measured by a matrix of correlation coefficients and the principal components extracted from the correlation matrix (see Davis, 1973, p. 152-168, 473-500, for explanation of principal components).

CALYX VOLUME, ARMS, AND PINNULES

The development of calyx volume and "size" follows an exponential pattern (Table 3). Youngest observed crinoids have "sizes" of 1.0 to 2.3 mm and volumes ranging from about 0.001 to 0.01 cc. Adults are distributed over a 5 to 13 mm "size" range and volumes of 0.1 to 1.0 cc. During early development, 1 mm increments of "size" resulted in small growth rates of volume, whereas in mature individuals the same "size" increments are correlated with much more rapid enlargements of volume. The exponents range from 2.8 to 3.4 compared with an ideal value of 3.0. The growth differentials are correlated with two factors. The first is the

calyx shape. In forms with wide calices relative to height, volume increased more rapidly than in those with slender calices (Table 3; compare equations 1, 5, 6 with 2-4). Second, for species with similar proximal calyx shapes, those with few fixed brachials show slower growth rates of volume than taxa with many fixed brachials (Table 3; compare equations 1 and 5).

The smallest specimens of most Girardeau camerates have similar calyx volumes and food-gathering systems. Typical figures are: calyx volume, 0.0006-0.001 cc; food-gathering-system length, 5.6-6.2 cm; five to nine brachials in a half-ray; pinnule length, 0.5-0.95 mm; and length of arms in a half-ray, 1.0-2.0 mm. Divergences occurred throughout later ontogeny and the food-gathering systems of mature crinoids commonly differed greatly.

New brachials were added to the arms throughout ontogeny and, as in living species, all new plates formed at arm tips. Generally all plates within a free arm bear pinnules except for one or two distal free brachials, free axillaries, and free brachials located immediately above the free axillaries. In the youngest crinoids, several of the proximal free brachials may lack pinnules. The number of brachials in the half-rays should scale as a linear dimension. The ideal exponent for development of number of brachials relative to calyx volume is 0.33. Except for *Ptychocrinus fimbriatus,* new brachials formed faster than in the ideal case (Table 4). The largest exponents

TABLE 3. *Growth of "Size" and Calyx Volume.*

[X = "Size" in mm; Y = Calyx volume in cc.]

EQUATION NUMBER	SPECIES	INITIAL INTERCEPT	EXPONENT	MINIMUM X	PREDICTED MINIMUM Y	MAXIMUM X	PREDICTED MAXIMUM Y	CORRELATION COEFFICIENT	NUMBER OF SPECIMENS
1	*Eopatelliocrinus scyphogracilis*	0.000754	2.78	1.15	0.00111	7.70	0.219	0.946	16
2	*E. latibrachiatus*	0.000689	3.33	1.15	0.00110	5.00	0.148	0.961	10
3	*Macrostylocrinus pristinus*	0.000588	3.39	1.00	0.000588	7.00	0.432	0.965	10
4	*Alisocrinus tetrarmatus*	0.000800	3.09	1.10	0.001070	6.70	0.285	0.971	12
5	*Ptychocrinus splendens*	0.001770	2.54	2.10	0.011600	12.70	1.12	0.917	16
6	*P. fimbriatus*	0.000723	2.76	2.30	0.007220	7.50	0.189	0.936	6

TABLE 4. *Growth of Calyx Volume and Brachials per Half-ray.*

[X = calyx volume in cc; Y = number of brachials per half-ray.]

EQUATION NUMBER	SPECIES	INITIAL INTERCEPT	EXPONENT	MINIMUM X	PREDICTED MINIMUM Y	MAXIMUM X	PREDICTED MAXIMUM Y	CORRELATION COEFFICIENT	NUMBER OF SPECIMENS
1	*Eopatelliocrinus scyphogracilis*	130	0.400	0.0007	7.09	0.220	70.9	0.954	16
2	*E. latibrachiatus*	136	0.386	0.0006	7.78	0.132	62.4	0.954	10
3	*Macrostylocrinus pristinus*	166	0.433	0.0003	4.94	0.237	89.0	0.985	10
4	*Alisocrinus tetrarmatus*	284	0.474	0.001	10.7	0.216	137.0	0.991	12
5	*Ptychocrinus splendens*	254	0.558	0.012	21.4	0.865	234.0	0.938	16
6	*P. fimbriatus*	71.4	0.268	0.006	18.1	0.184	45.4	0.970	6

are those of *P. splendens, Alisocrinus tetrarmatus* and *Macrostylocrinus pristinus.*

The developmental rate of new brachials in a half-ray or ray can be accelerated in several ways:

(1) Development of biserial brachials as in *Macrostylocrinus* (Patelliocrinidae) with two free unbranched biserial arms in each ray (Fig. 9). This augmented the number of brachials per unit length of free arm compared to crinoids with uniserial brachials of roughly the same height. For example, the number of brachials increased more slowly in the patelliocrinids which had two free, unbranched, uniserial arms than in those with biserial arms (compare Fig. 8 and 9; equations 1-3 in Table 4).

(2) Increase in the number of fixed or free arms. *Alisocrinus tetrarmatus* bears four free arms in each ray which are uniserial and unbranched; the fixed-axillary is secundibrach *2* (Fig. 10). The free brachials of the camerate *Alisocrinus* are similar to those of the patelliocrinids which have only two free arms in each ray. New free brachials developed much faster in *A. tetrarmatus* than in the patelliocrinids (compare Fig. 8 and 10; equations 1, 2, and 4 in Table 4). *Ptychocrinus splendens* usually has eight uniserial free arms in each ray with free axillaries located on secundibrachs *13-15* and tertibrachs *30-40.* This crinoid had the most rapid rate of formation of new brachials in all species that I have examined statistically (Table 4). Development of hypertrophied arms or ray trunks probably also accelerated the rate of formation of new free brachials. Unfortunately, there are no available statistical data, but this is suggested by qualitative observations on many species (see later annotation of *Ctenocrinus paucidactylus*).

(3) Retention of arms having the same length associated with development of shorter brachials. For example, mature *Eopatelliocrinus scyphogracilis* and *E. latibrachiatus* have approximately the same number of brachials but arms of the latter species are much shorter as are also the brachials (Tables 4, 5, equations 1, 2).

(4) Any combination of two or all three above-cited mechanisms. For example, many actinocrinitids have numerous branched free arms composed of short biserial brachials.

The crinoids with slower developmental rates, *Eopatelliocrinus scyphogracilis* (Fig. 8), *E. latibrachiatus,* and *Ptychocrinus fimbriatus* (Table 4, equations 1, 2, 6), all show two uniserial arms in each ray.

Inspection of any camerate shows that the length of a single free arm or the length of the arms in a half-ray increased with progressive age. This was controlled by addition of new brachials and height growth of previously formed plates. Except for *Ptychocrinus fimbriatus,* length increased more rapidly relative to calyx volume than in the ideal case (Table 5). The most rapid growth occurred in *Ptychocrinus splendens* with eight arms in a ray and in *Alisocrinus tetrarmatus* with four arms in a ray. The other taxa here considered show two uniserial or biserial arms in each ray. *Ptychocrinus fimbriatus* is characterized by the smallest growth rate, largely because of an extremely low rate of new brachial formation (Table 4, equation 6). The *Eopatelliocrinus* species and *Macrostylocrinus pristinus*

TABLE 5. *Growth of Calyx Volume and Free-arm Length within Half-ray.*

[X = calyx volume in cc; Y = arm length in mm.]

EQUATION NUMBER	SPECIES	INITIAL INTERCEPT	EXPONENT	MINIMUM X	PREDICTED MINIMUM Y	MAXIMUM X	PREDICTED MAXIMUM Y	CORRELATION COEFFICIENT	NUMBER OF SPECIMENS
1	*Eopatelliocrinus scyphogracilis*	59.8	0.475	0.0007	1.90	0.220	29.1	0.978	16
2	*E. latibrachiatus*	48.5	0.455	0.0006	1.66	0.132	19.3	0.968	10
3	*Macrostylocrinus pristinus*	53.1	0.480	0.0003	1.08	0.237	26.6	0.988	10
4	*Alisocrinus tetrarmatus*	114.0	0.556	0.001	2.44	0.216	48.8	0.990	12
5	*Ptychocrinus splendens*	98.3	0.629	0.012	6.09	0.865	89.7	0.949	16
6	*P. fimbriatus*	19.3	0.229	0.006	5.99	0.184	13.1	0.979	6

TABLE 6. *Growth of Calyx Volume and Average Pinnule Length.*

[X = calyx volume in cc; Y = average pinnule length in mm.]

EQUATION NUMBER	SPECIES	INITIAL INTERCEPT	EXPONENT	MINIMUM X	PREDICTED MINIMUM Y	MAXIMUM X	PREDICTED MAXIMUM Y	CORRELATION COEFFICIENT	NUMBER OF SPECIMENS
1	*Eopatelliocrinus scyphogracilis*	15.9	0.416	0.0007	0.772	0.220	8.46	0.974	16
2	*E. latibrachiatus*	8.84	0.315	0.0006	0.856	0.132	4.67	0.912	10
3	*Macrostylocrinus pristinus*	15.6	0.419	0.0003	0.520	0.237	8.53	0.976	10
4	*Alisocrinus tetrarmatus*	15.1	0.466	0.001	0.602	0.216	7.37	0.990	12
5	*Ptychocrinus splendens*	5.94	0.187	0.012	2.60	0.865	5.78	0.624	16
6	*P. fimbriatus*	6.68	0.211	0.006	2.27	0.184	4.68	0.653	6

developed new brachials at more rapid rates. The brachial heights of all taxa are roughly similar and the divergences in arm length between the Girardeau species mostly reflect the number of arms in a ray and the formation rates of new brachials.

Additional pinnules developed as new brachials became incorporated in the growing arms. The lengths of previously formed pinnules were increased by two mechanisms throughout ontogeny. New pinnulars grew at the distal pinnule tip. In most species examined, the average pinnules of young individuals have few pinnulars, whereas 10 or more occur in those of mature crinoids. The ideal exponent for ontogeny of pinnule length (a linear dimension) relative to calyx volume is 0.33. Long pinnules and relatively rapid growth rates of pinnule length were found in *Alisocrinus tetrarmatus, Macrostylocrinus pristinus,* and *Eopatelliocrinus scyphogracilis* (Table 6, Fig. 8-10). Dimerocrinitidae (e.g., *Ptychocrinus*) were characterized by short pinnules and slow developmental rates. *E. latibrachiatus* is intermediate between the two groups.

Because of the relationships between calyx volume, the food-gathering system and its components, the percentage of ambulacral tracts represented by pinnules rises rapidly during development of the crinoid. The pinnule percentage is determined by: [100 × (number of pinnule-bearing brachials per half-ray) × (average pinnule length) × (total number of half-rays)] ÷ (total length of food-gathering system).

The minimum pinnule percentages vary from 60 to 80 percent in the smallest studied crinoids depending on "size" and species. The mature specimen values equal about 94 to 96 percent of all Girardeau camerates.

ENTIRE FOOD-GATHERING SYSTEM

The length of the food-gathering system is a linear dimension which is mainly a product of two other linear dimensions, namely number of pinnulate brachials and average length of the pinnules. The length of the food-gathering system is calculated from: [(average pinnule length) × (number of pinnule-bearing brachials)] + (length of all free arms).

Arm length is negligible relative to length of the food-gathering system represented in the pinnules. For growth of length of food-gathering system relative to calyx volume, the ideal exponent is 0.67. As mentioned earlier, youngest crinoids have similar calyx volumes and lengths of the food-gathering system. However, the subsequent developmental story depends mainly on divergence in nature of the food-gathering systems in various species.

Ontogeny of length of food-gathering system relative to calyx volume is curvilinear in all Girardeau camerates in which the growth rates of length of food-gathering-system per 0.01 cc of calyx volume increment dropped with increasing volume and age, i.e., negative allometry (Table

7). Except for *Ptychocrinus fimbriatus,* the food-gathering system grows more rapidly than one would predict based on the ideal case. In *P. fimbriatus,* the food-gathering system develops more slowly than in the ideal case. In general, crinoids with pinnulate arms seem to have maximized the growth rates of the length of the food-gathering system with respect to calyx volume as much as possible within the inherent geometrical limits of the food-gathering system.

The "food-gathering ratio" equals (length of food-gathering system)/(calyx volume). These are calculated from the equations of length of the food-gathering system vs. calyx volume. The data are listed in Table 8.

Invariably, the food-gathering ratio declines during progressive development of a single species. The initial change is most rapid, since 50 percent or more of the total drop occurs during the lower 15 percent of the calyx volume range, whereas the remaining decrease is distributed over the latter 85 percent of the volume interval. The six species are divided into four gradational categories based on the growth patterns of the food-gathering system. These are listed below along with the contained species.

1) Rapid development of food-gathering system with exponents ranging from 0.87 to 0.92 (Table 7). *Alisocrinus tetrarmatus* has four uniserial arms in each ray with the resultant high rate of brachial addition in conjunction with long pinnules. *Macrostylocrinus pristinus* bears only two arms in each ray but the biserial brachials denote rapid brachial addition; long pinnules are also present.

2) *Eopatelliocrinus scyphogracilis* is characterized by an exponent of 0.81. Like the macrostylocrinid two arms are developed in each ray,

TABLE 7. *Growth of Calyx Volume and Length of Food-gathering System.*

[X = calyx volume in cc; Y = length of food-gathering system in cm.]

SPECIES	INITIAL INTERCEPT	EXPONENT	MINIMUM X	PREDICTED MINIMUM Y	MAXIMUM X	PREDICTED MAXIMUM Y	CORRELATION COEFFICIENT	NUMBER OF SPECIMENS
Eopatelliocrinus scyphogracilis	2134	0.807	0.0007	6.07	0.220	629	0.976	16
E. latibrachiatus	1337	0.717	0.0006	6.56	0.132	313	0.937	10
Macrostylocrinus pristinus	2900	0.872	0.0003	2.46	0.237	826	0.988	10
Alisocrinus tetrarmatus	4360	0.920	0.001	7.57	0.216	1060	0.996	12
Ptychocrinus splendens	1390	0.729	0.012	55.4	0.865	1250	0.912	16
P. fimbriatus	482	0.452	0.006	47.8	0.184	224	0.885	6

TABLE 8. *Food-gathering Ratios of Girardeau Camerates.*

[In calculating the means and coefficients of variation, the youngest *Ptychocrinus splendens* were omitted because their calyx volumes are much larger than the smallest specimens of the other species.]

SPECIES	FOOD-GATHERING RATIO cm/cc	
	YOUNGEST CRINOIDS	OLDEST CRINOIDS
Eopatelliocrinus scyphogracilis	8680	2860
E. latibrachiatus	10900	2370
Macrostylocrinus pristinus	8200	3490
Alisocrinus tetrarmatus	7570	4930
Ptychocrinus splendens	4610	1450
P. fimbriatus	7960	1220
Mean—all species	8660	2720
Coefficient of Variation—all species	15.2%	50.6%

but they are uniserial. Long pinnules occur.

3) Moderately slow developmental rates of food-gathering system are seen in *Ptychocrinus splendens* and *Eopatelliocrinus latibrachiatus* with exponents of 0.73 and 0.72. *Ptychocrinus* possesses extensively branched uniserial arms which cause a high rate of brachial addition, but the pinnules are quite short. The patelliocrinid pinnules are moderately long but only two uniserial arms are present in each ray.

4) *Ptychocrinus fimbriatus* exhibits the slowest growth rate of the food-gathering system among all crinoids studied, for its exponent is only 0.45. The growth rates of pinnule length and new brachials are both low because only two uniserial arms occur in each ray and the moderately tall brachials bear short pinnules.

In an attempt to evaluate ontogeny of the food-gathering system further, the approximate number of tube feet was computed for several individuals of *Alisocrinus tetrarmatus* (Table 9). For calculation, the tube-foot arrangement of *Antedon* (Nichols, 1960) is extrapolated to the camerate. Each pinnular covering plate is assumed to have been associated with three food-catching tube feet and each brachial covering plate probably housed a single feeding tube foot. In reality, the tube-foot order is not important as long as it was constant throughout growth. All Girardeau camerates have four or five pairs of covering plates on each brachial and pinnular (except terminal brachials and pinnulars for which the number is unknown). This distribution was retained during ontogeny where observed. The capacity for food-gathering, as measured by the number of feeding tube-feet in relation to calyx volume, decreased throughout ontogeny (Table 9). The initial downtrend of the ratio is most rapid, for more than half of the total decline occurs over roughly 5 to 10 percent of the calyx volume interval. It is notable that (length of the food-gathering system)/(calyx volume) and (number of food-catching tube feet)/calyx volume) behaved similarly during development. Both ratios decline as the crinoids become larger, indicating that the food-gathering capacity relative to volume dropped throughout growth. Continuation of this ontogenetic pattern could produce a "hypothetical crinoid" where the number of food-catching tube feet is too low and the food-gathering system too short to provide the volume of soft tissues with food. Obviously no crinoid reached this critical limit although some forms may have approached it. Perhaps some ratio of (length of the food-gathering system)/(tissue volume) or (number of food-catching tube feet)/(tissue volume) serves as a limit beyond which further increase of tissue cannot take place.

The food-gathering ratios of the Girardeau camerates are listed in Table 8. Those of the youngest crinoids are about the same with a mean for the studied species amounting to 8660 and a range of 7570 to 10,900 with a coefficient of variation of 15.2% (the dimension of the food-gathering ratio is cm/cc, although these are omitted in the text; the coefficient of variation is the standard deviation divided by the mean and expressed as a percentage). The relatively uniform food-gathering ratios may indicate that the youngest crinoids of all forms had similar stem lengths with the crowns located at the same elevation above the sea floor. If so, one would expect that similar natural selection operated on the food-gathering ratios of the youngest animals of all species. The food-gathering ratios of mature crinoids of different species vary greatly. These cover a 1220 to 4930 interval with a 2720 mean and 50.6% coefficient of variation (Table 8). This may imply more diversified adaptations

TABLE 9. *Ontogeny of Feeding Tube-feet in* Alisocrinus tetrarmatus.

"SIZE" mm	CALYX VOLUME cc	FEEDING TUBE-FEET PER ARM	FEEDING TUBE-FEET IN PINNULES OF SINGLE ARM	TOTAL NUMBER OF FEEDING TUBE-FEET	TOTAL NUMBER OF FEEDING TUBE-FEET/ CALYX VOLUME
1.1	0.001	150	60	4,200	4,200,000
1.4	0.002	180	150	6,600	3,300,000
4.2	0.20	1710	5700	148,000	740,000
5.5	0.20	1950	4550	130,000	650,000

of the adult crinoids. Possibly, the crowns of the various camerates occurred at different elevations above the sea floor. This cannot be verified for the Girardeau forms because complete stem lengths are unknown. However, Lane (1963b) showed that different crinoid species from the Crawfordville fauna formed a multilayered community as determined by stem lengths of the various taxa.

The abundant Girardeau camerates maintained large populations where small coefficients of natural selection comprised effective agents of evolution. This suggests that any consistent trend toward differential elimination of certain morphological types during ontogeny was produced by natural selection, which operated over the life of the crinoid. If so, the differential trends should be interpreted in terms of adaptation. The variation of length of food-gathering system relative to calyx volume was decreased throughout life. This is shown by comparing the percentage standard deviations of length of food-gathering system with respect to calyx volume (Brower, 1973, p. 324-325). The large decrease in percentage standard deviations from young to adult conspecific crinoids suggests that natural selection on the food-gathering ratio was most intense during the earlier growth stages. At any one growth stage, the direction of selection favored crinoids with high food-gathering ratios and operated against individuals with low food-gathering ratios. The direction of selection is inferred from the distribution of abnormal individuals. Three young crowns of *Alisocrinus tetrarmatus* have only three arms in one or more rays rather than the normal four. These had lower food-gathering ratios than normal individuals of the same calyx volume and "size." Only one such abnormal adult crown is known. Young *Ptychocrinus* with aborted arms or rays that failed to develop fully are fairly common. These abnormal forms also had low food-gathering ratios as compared with normal specimens of the same "size" and calyx volume. All adult forms of *Ptychocrinus* show normal arms and rays. The higher frequencies of abnormal youngsters suggest that these were eliminated by natural selection before attainment of maturity. Basically, it appears that natural selection acted against individuals with low food-gathering ratios. This is also supported by the probability that the young Girardeau camerates spent more time feeding than did the older animals. Similar natural selection can be documented for the Carboniferous inadunate *Woodocrinus macrodactylus*. Normal variants bear 20 arms, but about 15 percent of the observed specimens possess 21 to 35 arms. The life spans (in terms of relative age) of the crinoids with more than 20 arms are significantly longer than those of the typical 20-armed variants. In all of these lineages, the long-term evolutionary trends are toward more complex food-gathering systems and presumably toward a higher food-gathering ratio. It is notable that the directions of short-term ontogenetic selection and long-term selection for the entire lineages are the same.

Relative to an equivalent "sized" crinoid with an average or high food-gathering ratio, Girardeau camerates with low ratios exhibit lesser food-gathering and respiratory capacity owing to their shorter food-gathering system with fewer tube feet, reduced arm leverage because of the shorter food-gathering system with smaller surface area, and fewer gonads in some specimens. Which character or combination of characters was (were) selected for and against cannot be determined at present.

INTEGRATION AND COORDINATION OF GROWTH OF THE FOOD-GATHERING SYSTEM

The correlation coefficients for growth of food-gathering systems of camerate crinoids almost invariably exceed 0.87 and most are above 0.90; the associated significance levels are usually equal to or greater than 0.99 (Table 10). The high correlation coefficients and their significance levels indicate that the ontogeny of the food-gathering system of all forms was subject to a high degree of integration and coordination. Thus, the larger crinoids had longer food-gathering systems, greater calyx volumes, more pinnules and pinnulars, and longer arms. The lowest correlation coefficients, 0.62 to 0.91, are found in the ptychocrinids where pinnule length is involved; in these crinoids, the pinnule length was relatively ill-integrated and coordinated with development of the food-gathering system, "size," and calyx volume.

The overall degree of integration and coordi-

nation among species is shown by ranges of the correlation coefficients and percentages of correlation-matrix variance associated with the first principal components extracted from the correlation matrix (Table 10, see Davis, 1973, p. 152-168, 473-500, for explanation of principal components). The first principal component of all species is an overall growth factor. This is reflected by the principal component scores which array the crinoids in order of increasing "size" and calyx volume. The coefficients for all variables are nearly equal. Basically the first principal component extracts the correlations between all variables and most of the size and shape growth of the crinoids. From 89.4 to 98.7 percent of the variance in the correlation matrix can be attributed to the overall growth factor in the different species.

Assuming that adequate support was provided by the calyx, the explanation of the overall high degree of integration and coordination of the food-gathering system of camerates is easily visualized from several geometrical and functional relationships. The free arm length and number of brachials are positively correlated. In turn, these were both partially controlled by the growth of the free-brachial dimensions. Basically, the problem involves mechanics: how many brachials bound together by ligaments can be arranged from bottom to top before the structure becomes unstable? Pinnule length and size and area of the pinnule facet are clearly related to one another, inasmuch as the facet supports the pinnule. In turn, the area of the pinnule facet and its rate of increase is dictated by growth rates of the free-brachial parameters. Also, the length of the food-gathering system in a half-ray is highly coordinated and integrated with the supporting area of the distal fixed brachial. In turn, the development of these plates can be related to the growth of calyx size. The calyx "size" and volume show a high degree of integration because the growth of "size" and the component calyx plates determine increased calyx volume and enlargement of the visceral mass. Functionally, the food-gathering system supplies the viscera with food and, to some extent, oxygen. Because of their complex geometrical and functional interrelationships, the development of the food-gathering system comprises a highly integrated and coordinated package.

The highest correlation coefficients and largest percentages of correlation-matrix variance associated with the first or growth principal component are found in the four monocyclic species. All of these crinoids possess closely knit patterns of development. A slight gradient extends from *Alisocrinus tetrarmatus* with highest degree of regulation to *Eopatelliocrinus latibrachiatus* with least. The second principal component extracts "size" variation that is independent of the other parameters. Examination of the correlation coefficients and percentage standard deviations indicates that growth of food-gathering systems and their components is more highly correlated with and less variable with respect to calyx volume than the linear dimension "size" in these species. Obviously, this is due to the fact that calyx volume more closely reflects the amount of tissue that must have been supplied with food than does "size."

A different situation is seen in the *Ptychocrinus* specimens where lower correlation coeffi-

TABLE 10. *Integration and Coordination of Food-gathering-system Growth in Girardeau Camerates.*

SPECIES	NUMBER OF SPECIMENS	RANGE OF ALL CORRELATION COEFFICIENTS	RANGE OF CORRELATION COEFFICIENTS INVOLVING "SIZE"	RANGE OF CORRELATION COEFFICIENTS INVOLVING CALYX VOLUME	CORRELATION-MATRIX VARIANCE ACCOUNTED FOR BY FIRST PRINCIPAL COMPONENT IN PERCENT
Alisocrinus tetrarmatus	12	0.970–0.996	0.970–0.981	0.971–0.991	98.7
Macrostylocrinus pristinus	10	0.952–0.996	0.952–0.967	0.965–0.988	98.2
Eopatelliocrinus scyphogracilis	16	0.893–0.994	0.893–0.946	0.946–0.978	96.5
E. latibrachiatus	10	0.868–0.995	0.868–0.961	0.912–0.968	95.1
Ptychocrinus fimbriatus	6	0.653–0.987	0.690–0.977	0.653–0.979	89.6
P. splendens	16	0.624–0.974	0.725–0.948	0.624–0.949	89.4

cients occur in conjunction with lesser amounts of variance involved in overall size increase. This discloses a less sophisticated and less well-regulated growth pattern in these species. The second principal component of these taxa is associated with size-independent variation in pinnule length. The pinnule length correlations are low and this character is poorly integrated into the developmental mosaic.

Perhaps notable is the observation that the contrasting growth patterns of the six species considered can be related to taxonomy and phylogeny. The four monocyclic crinoids are related and all share a similar highly integrated pattern of ontogeny. The two dicyclic ptychocrinids are only distantly allied with the monocyclic forms. The former crinoids are characterized by a different growth pattern, which was less well regulated. The degree of integration and coordination, as measured by percentage of the correlation-matrix variance involved in the first principal component, and the rate of growth of the food-gathering system as determined by the exponent taken from the equation of length of the food-gathering system vs. calyx volume (Table 7) are positively correlated with a 0.824 coefficient, which is significant at the 0.950 level. The data suggest that a certain rate of growth of the food-gathering system requires a critical threshold level of integration and coordination.

RAY TRUNKS

The preceding discussion applies to camerate crinoids with normal pinnulate arms. Many of these, such as melocrinitids, the actinocrinitids *Steganocrinus* and *Cytidocrinus,* the dimerocrinitid *Lampterocrinus,* and the platycrinitid *Eucladocrinus,* evolved hypertrophied arms or ray trunks. Ray trunks consist of massive nonpinnulate arms which bear pinnulate branches. Where well developed, a long food-gathering system is present with numerous branches arranged in a complex pattern. Generally, similar ray trunks are developed in various unrelated crinoids. They were produced by convergent evolution in response to selection pressures favoring more complex food-gathering systems. Size increase commonly accompanies increased complexity of the food-gathering system. The two characters appear to be closely linked, for more complex food-gathering systems allow development of larger crinoids and such size increase requires a more complex food-gathering system. Thus, the basic selection pressure in these lineages was possibly for increased size. The common denominator of growth is acceleration of the ray-trunk ontogeny relative to "size" and other dimensions.

Ontogeny is best known in the Devonian melocrinitid *Ctenocrinus paucidactylus* (Goldring, 1923, p. 122-125, pl. 8, fig. 5, pl. 9-11; Ubaghs, 1958, p. 293-304; Fig. 19). The development of this form should be compared with that of its remote ancestor, the Ordovician *Alisocrinus tetrarmatus* (Fig. 10; see discussion in Ubaghs, 1958, p. 293-304; Brower, 1973).

Many melocrinitids, including *Alisocrinus* and *Ctenocrinus,* basically have four branched or unbranched arms in each ray with axillary fixed-secundibrach *2,* rarely *3.* In *Alisocrinus,* all four arms are uniserial, unbranched and pinnulate (Fig. 10). The outer two arms of a mature ray in *Ctenocrinus paucidactylus* resemble those of *Alisocrinus* (Fig. 19,*4-6*). Although the inner two arms of a *C. paucidactylus* ray are hypertrophied into massive and extensively branched ray trunks, they are clearly homologous with the inner two arms of an *Alisocrinus* ray (compare Fig. 10 and 19; see Ubaghs, 1958, and Brower, 1973, for discussion of homologies and phylogeny). The uniserial brachials of the ray trunks lack pinnules. The ray trunks bear numerous ray-trunk branches which consist of uniserial pinnulate brachials in *C. paucidactylus.*

FIG. 19. Growth sequence of *Ctenocrinus paucidactylus,* Lower Devonian, New York, a glyptocrinid-type calyx having ray trunks, crinoids arranged in order of increasing "size" (Goldring, 1923).

1. *CD*-interray view of young crinoid with pinnule-like ray trunks, ×3.
2. Side view of young crown with immature ray trunks which bear several branches, ×3.
3. Side view of young crinoid with ray trunks just beginning to join, ×2.
4. Side view of specimen similar to that shown in *3,* ×2.
5. Side view of young adult with almost fully joined ray trunks, ×1.
6. Side view of mature adult with fully developed ray trunks, ×1.

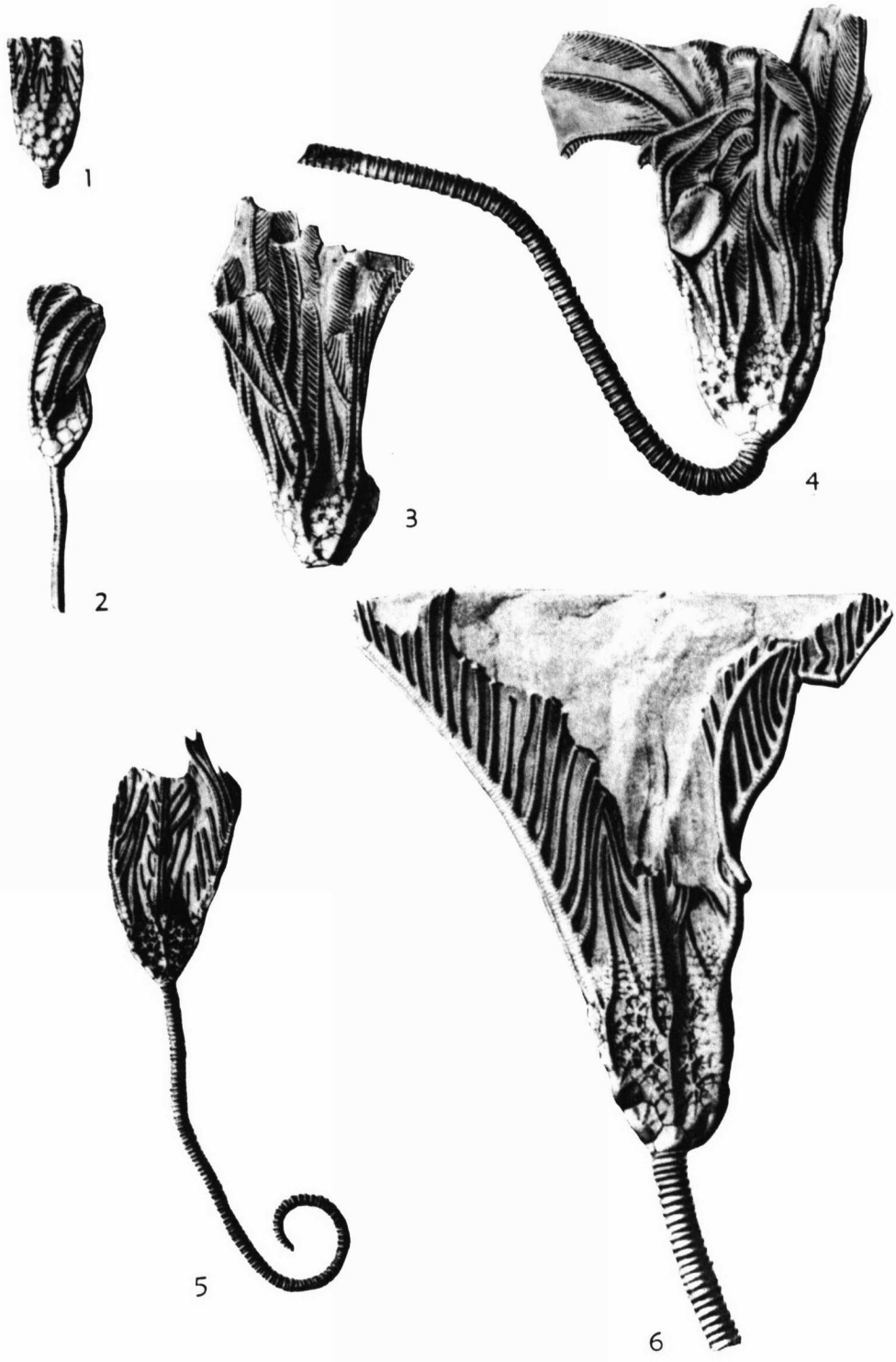

FIG. 19. *(For explanation see facing page.)*

The outer two arms of a ray in the youngest *Ctenocrinus paucidactylus* are well developed and fully pinnulate (Fig. 19,*1*). The inner arms are smaller, nonpinnulate, and resemble pinnules; their size is probably underestimated in Goldring's figures because they are partially buried in matrix (Ubaghs, 1958, p. 297). At this point, the outer arms of a single ray in the ancestor and descendant are at comparable growth stages but the inner arms of *C. paucidactylus* are reduced or retarded (compare Fig. 19,*1* with Fig. 10,*1-3*). During later growth, the inner arms of the *Ctenocrinus* underwent accelerated ontogeny and developed into ray trunks (Fig. 19,*2-6*), but the outer arms remained normal pinnulate arms throughout life. New uniserial brachials were added at the distal arm tips of all free arms but these developed most rapidly in the ray trunks, at least three times as fast as in the outer arms. Unlike brachials in the outer arms, the brachials of the ray trunks failed to form pinnules. New branches of the ray trunks were initiated while new brachials formed at tips of the ray trunks. The first branch in *Ctenocrinus paucidactylus* is found on or near tertibrach *10* and higher branches on the ray trunks are separated by five to nine brachials. Mature crinoids bear more than 20 branches on the ray trunks. The brachials of the branches on the ray trunks are uniserial and pinnulate in *C. paucidactylus,* but some forms such as *Trichotocrinus* have biserial pinnulate brachials. In *C. paucidactylus,* the rate of new plate formation in the ray trunks, including brachials of the ray trunks and branches of the ray trunks and pinnulars, as in the ray trunks, was at least 10 times more rapid than in the outer arms where only tertibrachs and pinnulars are present. Thus the development of ray trunks resulted in a rapid rate of plate supply compared to a normal arm. During the later development stages of *C. paucidactylus* (Fig. 19,*5,6*), the adjacent ray trunks began to fuse together to provide better support for the branches and pinnules of the ray trunks. This process operated from proximal to distal extremities of the arms.

GROWTH OF SUPPORTING STRUCTURES

Until now, the ontogeny of the supporting elements has been studied only in three Girardeau species. Presently available data are recalculated from Brower (1973) using simple power functions and some additional measurements. A crinoid endoskeleton is a complex of supporting relationships. Essentially, each plate bears all higher ones. For example, the proximal columnal supports the crown, basals underlie the radials and all higher plates, distal fixed brachials elevate the arms, and pinnule facets hold the pinnules. Owing to limits of time and preservation, not all supporting relationships can be evaluated and attention is focused on the proximal columnal area and the area of the distal fixed brachial.

One key supporting structure is the proximal columnal which elevates the effective mass of the crown. This is approximated by development of the proximal columnal area relative to calyx volume which has an ideal exponent of 0.67. The approximation is justified because both the effective mass of the crown and the calyx volume are volume functions which should scale similarly during growth. The observed exponent of *Eopatelliocrinus scyphogracilis* somewhat exceeds the ideal value but those of the other two taxa are slightly less than 0.67 (Table 11). Note that range of the initial intercept for *E. scyphogracilis* is twice as large as those of the other crinoids. The youngest crinoids all have similar supporting ratios, i.e., (area of proximal columnal)/(calyx volume). Throughout ontogeny, the supporting ratio declined and mature crinoids were "less well supported" than youngsters. Seemingly, continuation of this decrease eventually could have produced a stem too small to have elevated and supported the crown. Actually, the undefined ratio of stem area to effective mass of the crown must have represented the critical factor and possibly a certain ratio provided a limit to size growth. Whether or not any camerate reached this limit is speculative. The bulk densities of the crowns of the three Girardeau species were about 1.43 gm/cm^3 (Brower, 1973, p. 283-285). The observed ratios of adult proximal columnal area/calyx volume suggest that *Macrostylocrinus* (3.4) and *Alisocrinus* (2.8)

TABLE 11. *Growth of Proximal Columnal Area and Calyx Volume.*

[X = calyx volume in cc; Y = area of proximal columnal in mm².]

SPECIES	INITIAL INTERCEPT	EXPONENT	MINIMUM X	PREDICTED MINIMUM Y	MAXIMUM X	PREDICTED MAXIMUM Y	(MINIMUM PREDICTED Y)/(MINIMUM OBSERVED X)	(MAXIMUM PREDICTED Y)/(MAXIMUM OBSERVED X)	LOWEST OBSERVED Y/X RATIO FOR ADULT CRINOIDS	CORRELATION COEFFICIENT	NUMBER OF SPECIMENS
Eopatelliocrinus scyphogracilis ..	9.87	0.741	0.001	0.0591	0.318	4.22	59.1	13.3	13.0	0.964	8
Macrostylocrinus pristinus	4.70	0.660	0.0009	0.0458	0.349	2.35	50.9	6.72	3.41	0.950	12
Alisocrinus tetrarmatus	4.35	0.589	0.001	0.0745	0.953	4.22	74.5	4.43	2.76	0.975	11

TABLE 12. *Growth of Supporting Brachial Area and Length of Food-gathering System in One Arm.*

[X = length of food-gathering system in one arm in mm; Y = area of supporting brachial in mm².]

SPECIES	INITIAL INTERCEPT	EXPONENT	MINIMUM X	PREDICTED MINIMUM Y	MAXIMUM X	PREDICTED MAXIMUM Y	(MINIMUM PREDICTED Y)/(MINIMUM OBSERVED X)	(MAXIMUM PREDICTED Y)/(MAXIMUM OBSERVED X)	LOWEST OBSERVED Y/X RATIO FOR ADULT CRINOIDS	CORRELATION COEFFICIENT	NUMBER OF SPECIMENS
Eopatelliocrinus scyphogracilis	0.00432	0.629	7.40	0.0152	485	0.210	0.00205	0.000432	0.000412	0.913	12
Macrostylocrinus pristinus	0.0122	0.570	1.85	0.0173	320	0.327	0.00937	0.00102	0.00128	0.936	9
Alisocrinus tetrarmatus	0.0196	0.635	3.10	0.0401	615	1.15	0.0129	0.00188	0.000983	0.925	10

might have approached this limit, but *E. scyphogracilis* (13.0) was well above the critical ratio.

Basically, each arm is borne by the distal fixed brachial. Plotting the distal face area of the supporting brachial vs. the effective mass of the arm and its pinnules would illustrate the necessary relationship. This is approximated by growth of length of food-gathering system within a single arm and supporting brachial area. As mentioned earlier, both the length of the food-gathering system (mainly a product of two linear dimensions, namely the number of pinnule-bearing brachials in the arms multiplied by length of the average pinnule) and any area should have an ideal exponent of 2.0 relative to a linear dimension. Thus the ideal exponent for ontogeny of supporting brachial area with respect to length of the food-gathering system amounts to 1.0. Table 12 discloses that the supporting brachial of all taxa developed more slowly than expected, with exponents ranging from 0.57 to 0.64. The supporting ratio, (supporting brachial area)/(length of food-gathering system), decreases throughout development of all three species. Obviously, the ratio of (supporting brachial area)/(effective mass of the arm and pinnules) must have declined also with progressive age. Probably, continuation of this pattern eventually would have resulted in arms which were too long and heavy for the crinoid to support. Per-

haps, a critical ratio provided a limit beyond which further size growth could not have proceeded. Whether or not any of the Girardeau taxa approached or reached this limit is not known. However, the smallest ratios of supporting brachial area to length of food-gathering system are observed in adult *Eopatelliocrinus scyphogracilis,* which implies that this crinoid is closest to the limit. The mature *Macrostylocrinus* and *Alisocrinus* are characterized by larger ratios. The largest ratios are generally found in *Alisocrinus tetrarmatus,* which has four arms in each ray, whereas the other crinoids have only two. Possibly, increasing the number of arms may have resulted in a larger size limit. This is consistent with my observations on Mississippian platycrinitids and dichocrinids where larger forms tend to have more arms than smaller species in any one fauna (Brower, 1969, p. 517-521). However, the largest adult "sizes" of these Girardeau crinoids are all similar (9.0 to 12.6 mm). Perhaps, such augmentation of arm number was prerequisite and preadaptive to the larger size limit.

Comparison of the overall data on the supporting structures suggests that the terminal size of *Alisocrinus* may have been dictated by the proximal stem area, whereas the supporting brachial served this purpose in *Eopatelliocrinus scyphogracilis.* The final "size" of the macrostylocrinid may have been limited by both the stem and supporting brachial areas.

All three taxa show a highly correlated pattern of development of the supporting structures. The correlation coefficients range from 0.91 to 0.98 and their significance levels invariably exceed 0.999. The few available data suggest that the degree of integration and coordination decreases distally (Tables 11, 12).

GROWTH OF COLUMN

This discussion provides only a generalized summary. For more detail on the crinoid column and columnal growth, reference may be made to Wachsmuth & Springer (1897, p. 39-52), Bather (1900, p. 105-108, 131-136), Biese (1927), Termier & Termier (1949), Moore & Jeffords (1968), Jeffords & Miller (1968), Seilacher *et al.* (1968), and Brower (1973, p. 298-299).

The growth of a columnal follows the same pattern in both living and fossil crinoids (Fig. 20,*1,2*). The axial nerve cord penetrates the center of the columnals and passes through the axial canal. As in other plates, the axis of this structure forms a constant point of topographic reference. During ontogeny, the diameter of the axial canal is augmented by marginal resorption. The various growth rates are revealed by longitudinal sections of stems (e.g., Moore, Jeffords, & Miller, 1968, pl. 2, fig. 1, 2; see also pl. 3; various illustrations in Moore & Jeffords, 1968; Jeffords & Miller, 1968). The principal direction of calcite addition is outward or peripheral. The much smaller vectors of growth in proximal and distal height are symmetrical for columnals with and without cirri. Both nodals and internodals appear and grow rapidly. As the columnals mature, the developmental rates decrease to almost nil. Most camerate columnals have crenulate sutures which interlock adjacent columnals. Typically, the culmina or ridges are arranged in a radiating pattern (e.g., Jeffords & Miller, 1968, pl. 3). As height and width of the columnals increase, widths of the culmina are augmented and new ones are intercalated between older ones.

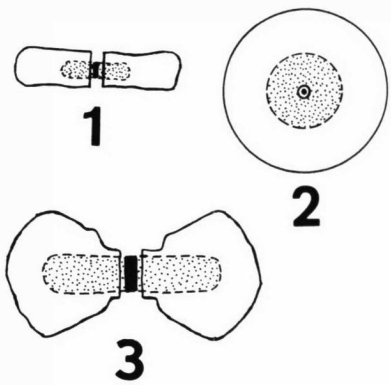

FIG. 20. Diagrams of superposed columnals showing growth stages (axial canal, black; smaller plate stippled with dashed outline; larger columnal shown by solid line).——*1, 2.* Schematic camerate columnals with flat articular surfaces, not to any scale, in side and axial plane views (Brower, 1973).——*3.* Side view of two *Pisocrinus campana* columnals, Middle Silurian, Scotland, not to scale (Brower, n).

During development of most living and fossil crinoids, new plates form in the stem. Typically some of these are initiated immediately below the calyx (nodals), whereas others grow between previously formed columnals (internodals). In most camerate crinoids which I have examined, more than half of the columnals form by intercalation. In a few crinoids (e.g., some *Pisocrinus*) all new columnals are developed just below the calyx.

The function of a crinoid stem is to elevate the crown above the substrate. Elevation is progressive and continues throughout life of a stalked crinoid. The rate of elevation is dictated by two growth vectors—the rate of initiation of new columnals and the growth rates of height in the old ones. During growth, crinoid stems must achieve a balance between two factors—suitable rate of lengthening and maintenance of an appropriate amount of flexibility in the column. Flexibility allows the crinoid to bend the stem so as to attain advantageous feeding orientation and to avoid undue stress on the column which might break the stem (Brower, 1973, p. 283-290, 298-299). Most camerates show the usual flexibility gradient seen in stalked crinoids. The amount of flexibility is measured by the radius of curvature shown by various parts of the column (Seilacher, *et al.,* 1968). In conventional stalked crinoids, including most camerates, many living and fossil isocrinids, most inadunates and flexibles, maximum flexibility generally occurs in the middle 67 to 75 percent of the column. Relatively rigid stem segments are associated with the rooting device and immediately below the calyx. This allows the crinoid to flex the stem against a rigid holdfast, thus achieving maximum mechanical leverage. With a certain articular type, column flexibility is directly proportional to the ratio of the ligament volume/external columnal volume. Crinoids possess several ways of obtaining a flexible stem, as described below.

(1) Growth of width in the columnals tends to decrease stem flexibility and, conversely, intercalation of new columnals increases it (Seilacher *et al.,* 1968). In most stalked crinoids, flexibility of the middle part of the stem is largely maintained by intercalation. The relatively rigid proximal and distal regions of the stem are mostly due to wide columnals and a low rate of columnal intercalation. Most stalked crinoids have relatively flat articular surfaces that are not strongly depressed throughout life. Within the stem, the most immature plates are those most recently intercalated, whereas later growth of height and width produces mature plates. Immature plates have higher ratios of ligament volume to external columnal volume than mature plates, roughly 7 to 10 percent in Girardeau camerates. Consequently, a continuous supply of new plates is required to maintain a flexible stem.

(2) All columnals of *Pisocrinus campana* (Fig. 20,*3*), an inadunate from the Silurian near Edinburgh, Scotland (Brower, in preparation), formed just below the calyx. Immature columnals are thin and disc-shaped. The volume of the ligaments relative to external volume of the columnal is uncertain but clearly did not exceed 7 percent. During later growth, height and width of the columnals were augmented and mature columnals are barrel-shaped. Growth in height allowed development of strongly depressed articular surfaces with large ligaments which occupied roughly 8.5 percent of the external volume of the columnal. The observed bends in the stem indicate that maximum flexibility was associated with the barrel-shaped columnals. The growth of these depressed articular surfaces was not due to resorption. Rather, the growth vectors of height increase are larger toward the outsides of columnals, thus forming depressed articular surfaces.

(3) It is possible that columnal intercalation and development of depressed articular surfaces were combined in many crinoids.

GROWTH OF ORNAMENTATION

Most camerate crinoids followed all or part of a three-stage sequence in surface ornamentation characteristics. During the first stage, plates were smooth and featureless. Next, median-ray ridges were formed, beginning on the primibrachs. These were later extended proximally, eventually reaching the base of the calyx. The last median-ray elements to appear were horizontal ridges which linked adjoining radials. Within the third and last phase, the ornamentation, such as stel-

late ridges, spines, nodes, etc., was initiated on interbrachials. The exact development sequence of these elements is unknown because they grew rapidly.

COMPARATIVE ONTOGENY OF CAMERATES AND LIVING CRINOIDS

Camerates and Recent crinoids show the same growth sequence of plates with respect to the arms, column, and most calyx plates. In many living crinoids (comatulids), the animal discards the column at the end of the pentacrinid growth stage and assumes a more or less free-living existence. This does not occur in camerates and Recent isocrinids, where, barring traumatic accidents, all or part of the stem is retained until death. Nevertheless, growth of the larval column in a comatulid and the camerate and isocrinid stem follows the same pattern. Columnals typically form immediately distal to the calyx, below the centrodorsal in pentacrinid growth stages of comatulids and below the infrabasals or basals of camerates. Also new columnals are generally intercalated between previously formed plates. All brachials and pinnulars first appear at distal tips of the arms or pinnules, although the proximal pinnules of camerates developed earlier than those of Recent species. The sequences of calyx-plate development in camerates and comatulids are the same except for proximal interbrachials. During the ontogeny of most camerates, free brachials become incorporated in the calyx, although at rates varying with calyx type. This does not occur in modern crinoids, among which the arms remain free above the radials throughout life. Typically the interprimibrachs *1* of Recent crinoids develop late in ontogeny, usually after primibrach *2* is present or still later. In camerates, these proximal interprimibrachs probably are initiated along with or soon after the radials. Camerate crinoids were probably also characterized by early development of the primanal. It is notable that the contrasts between the plate-growth sequences of living crinoids and camerates can be correlated with the presence or absence of fixed brachials.

Growth of the calyx plates in camerate and modern crinoids follows different paths. In camerates, the calyx base is floored by infrabasals in dicyclic forms and basals in monocyclic forms. The calyx walls are composed of the higher plates including radials, fixed brachials, interbrachials, and anals. The food grooves and distal part of the viscera were roofed by tegminal plates. Most camerate crinoids probably had a calcitic convoluted organ located inside the calyx. I believe that this structure both supported the gut and separated it from the chambered organ and aboral nerve cords. If so, the convoluted organ of camerates served roughly the same purpose as the basal rosette in comatulids. At any rate, the basic functions of the camerate calyx are to enclose, protect, and support the viscera, and to bear the free arms. These free arms are supported by distal fixed brachials, which in turn rest on more proximal plates. All calyx plates of camerates performed more or less the same functions.

Consequent to this functional morphology, major resorption was rare in calyx plates of camerates. I believe that resorption in camerate calyx plates is largely confined to plates located near the openings for free arms, anus, and axial canal of the column.

As noted by Clark (1915, p. 344-348), comatulids depart greatly from the camerate plan. The principal specializations of comatulids are related to reduction of the cup plates and increase in cup strength (see Fig. 4,*1* for cross section). Different parts of the comatulid cup serve different functions. The comatulid infrabasals, if present, are reduced. Early in ontogeny these fuse with the distal columnal to form the centrodorsal with cirri which the crinoid uses to grasp the substrate or foreign objects after the column is discarded. The comatulid basals are also insignificant cup elements which are metamorphosed and shifted upward to form the basal rosette during growth. The mature chambered organ is almost completely enclosed within the centrodorsal on its base and sides, by radials on its sides, and the basal rosette at its top. The viscera proper (i.e., inner and outer coelom, gut, etc.) rest on the distal margin of the basal rosette and radials. Thus, the basal rosette serves as a plat-

form which largely separates the chambered organ from the viscera proper. The principal function of the comatulid radials is probably to support the arms which are free above the radials. Lateral protection and support for the viscera proper are provided by the primibrachs. Thus in comatulids and to a lesser extent in isocrinids, the infrabasals, basals, and radials do not serve to support and protect the sides of the viscera as in camerates. Consequently, the growth patterns of the cup plates of modern crinoids and less complex camerates diverge. As mentioned above, resorption is rare in calyx plates of camerates. Conversely, in comatulids (isocrinid ontogeny is not well known), resorption during growth of the cup plates is common and can be documented for basals, centrodorsals, radianal, orals, and other tegminal plates (Clark, 1915, p. 322-340).

The initially formed radials of comatulids have flat inner and outer surfaces with axial nerve cords located inside of the plates (Fig. 7,*4-6*). Throughout ontogeny, calcite is deposited on the inside of the comatulid radials. In later growth stages of the radials, calcite deposition builds up the internal margins of the plates and the axial nerve cords occur in a groove on the inner side of the plates. Continued inward calcite deposition completely buries the axial nerve cords within the radials in the last development stage (Carpenter, 1866, p. 738-741). Growth of comatulid brachials follows the pattern established for radials (Fig. 16). In camerates, calcite is not deposited on the interior of the calyx plates and the axial nerve cords are housed on plate interiors throughout life (Fig. 7,*1-3*). Growth of the brachials produces a distal extension of the calyx plate type (Fig. 15,*5-8*) and the axial nerve cord lies at the base of the brachial food grooves regardless of age.

Morphologically, the radial is considered the base of a ray. This plate has paramount importance in taxonomy and phylogeny. It is also notable that the growth patterns of radials and brachials are basically the same for any one crinoid. The radials develop before the brachials in all crinoids and it seems that the growth types of the radial dictate the mode of brachial ontogeny. Clearly, this reinforces and explains the significance of the radials.

The camerate type of uniserial brachial growth predominated in the Paleozoic, whereas living forms are characterized by the comatulid type. This suggests progressive evolution and adaptation. Obviously, the Recent crinoid axial nerve cords are better protected. Damage to the food-groove tissue need not harm the axial nerves. This is important because the aboral nervous system, including axial nerve cords of the arms, is the major level of the nervous system which controls posture and other basic reactions. Conversely among camerates, many injuries to the food-gathering structures probably also damaged the axial nerve cords. Geometrically, the growth pattern of comatulids is far more complex than that of camerates. This implies that comatulid brachials require a higher degree of developmental integration and coordination than camerate plates. At present, this can only be suggested because necessary statistical data have not been compiled. If true, this may explain partially why camerates retained their type of growth, despite vulnerability of their axial nerve cords.

Some Paleozoic crinoids such as cyathocrinitids had nonpinnulate uniserial brachials with axial nerve cords housed within as in living species. Judging from their diversity and abundance, they were not so successful as contemporary camerates and other crinoids with camerate-type growth patterns of the brachials. Apparently the disadvantages of lack of pinnules outweighed the advantages of superior protection of the axial nerve cords.

Compared to cup or calyx plates and brachials, the main growth patterns of columnals are highly conservative. As far as can be determined, these are uniform in living crinoids and all fossil forms.

SUMMARY

Relatively complete sequences of ontogeny have been known in camerate crinoids for many years, although few papers have considered the growth of these forms. Generally, these growth stages range from immature specimens with four to eight brachials in each free arm and "sizes" of about 1.0 to 1.5 mm to adults with over 100 brachials in each arm and "sizes" that

vary from 5.0 to 75 mm. The growth stages of microcrinoids (prebrachiate crinoids) have been studied for specimens that are questionably assigned to the camerate crinoid *Cyttarocrinus eriensis* (Hall), a Devonian platycrinitid. Aside from the facts that the plates joined earlier and the arm facets were initiated in a different sequence, these microcrinoid growth stages are similar to those of extant species.

With a single exception, the developmental sequences of plates in camerates and Recent crinoids are the same. The first plates to form are the basals and orals. These are followed by the infrabasals (if present), radials, primibrachs *1* and *2,* secundibrachs *1, 2, 3,* and so on. All arm plates and pinnulars develop in a proximal to distal sequence so that all new plates are initiated at an arm or pinnule tip. New plates are never intercalated between older ones. Conversely, during ontogeny of the stem, some new plates first appear immediately below the calyx, whereas others are intercalated between previously formed plates. The first interprimibrach of camerates developed prior to the equivalent plate of extant crinoids. This is directly correlated with the presence of fixed brachials in camerates and the absence of these plates in living forms. The calyces of camerate crinoids are subdivided into five types based on the type of interbrachials, the distal extent of fixed brachials, and the number of arms. Xenocrinids show numerous small and irregular interbrachials; consequently, many of these plates were initiated by intercalation between older interbrachials. The interbrachials of all other camerates are large and regular, and development by intercalation is unknown. Some camerate crinoids have small groups of widely spaced arms, whereas others show more numerous arms that are relatively evenly spaced. Fixed brachials are extensive in some forms and almost absent in others. Despite the diversity of calyx types in adult crinoids, the youngest camerates are all similar. The differences between the adults are produced by divergences throughout subsequent ontogeny. Study of the sequence of calyx types throughout the Paleozoic indicates that calyces with few fixed brachials were the most successful.

All crinoids show the same type of columnal growth. However, the developmental patterns of the calyx and arm plates are strikingly different in camerate and Recent crinoids. The axial nerve cords of camerates are housed on the interior side of the plates throughout life. The pattern of calcite accretion is simple and seems designed to cause the minimum amount of interference with the aboral nerve cords. Modern crinoids are characterized by a more complex pattern of ontogeny. The embryonic axial nerve cords lie along the interior of the plates like those of camerates. Throughout subsequent ontogeny, modern crinoids diverge from camerates in that calcite deposition gradually buries the axial nerve cords within the plates. Resorption is much more common in living crinoids than in camerates. These divergences are partially related to differences in functions of the calyx plates in camerate and living crinoids. All camerate calyx plates enclose, protect, and support the viscera, and support the higher plates and free arms. Most camerates have a calcitic convoluted organ inside the calyx. Probably, this structure served to support the gut and separate it from the chambered organ and axial nerve cords. The important point is that all calyx plates of camerates performed the same general functions. Modern crinoids show more specialization and the various calyx plates are used for different purposes. For example, the radials support the free arms, the centrodorsal bears the grasping cirri, and several plates form the basal rosette which serves as a septum separating the chambered organ from the viscera proper. Thus the geometry of modern crinoids is more complex and therefore requires a higher degree of flexibility of ontogenetic patterns. This at least explains the fact that resorption is much more common in modern crinoids than in camerates.

In all crinoids, the growth types of the radials and brachials are the same. The axial nerve cords of camerates are housed at the base of the food grooves throughout life. The brachials of camerate crinoids are of two types. Uniserial brachials are characterized by gradual incremental growth and little resorption. On the other hand, the ontogeny of biserial brachials is more complex and resorption occurs while the brachials change from the uniserial to the biserial growth stages. Although the developmental pattern of biserial brachials is more complex, biserial brachials have two advantages over uniserial types—a closer packing of pinnules and enhanced food-

gathering capacity along with greater flexibility. During the history of camerates, the general evolutionary trend is from uniserial to biserial arms.

All modern crinoids have uniserial brachials, probably because of the nature of their articular surfaces. Throughout ontogeny, the axial nerve cords are buried within the brachials as in the radials. In the mature stage, the axial nerve cords are housed in canals inside the plates. Although the growth pattern of uniserial brachials in modern crinoids is more complex and requires a higher degree of developmental integration and coordination than in camerates, the axial nerve cords are much better protected. Inasmuch as the radials and brachials share the same growth pattern, this may also partially explain the divergence in ontogeny of brachial and calyx plates between camerate and living crinoids. The ultimate control of plate growth in crinoids is probably mesodermal. For the arm, stem, and ray plates of the calyx, this control may be indirect, in which the mesoderm operates by means of the axial nerve cords. Growth of tegmen plates which are not in contact with any of the crinoid nervous systems is presumably directly regulated by the mesoderm.

During ontogeny, the length of the food-gathering system of a camerate crinoid increases through addition of new brachials and pinnulars at the distal extremities of the arms and pinnules and height growth of previously formed plates. Based on geometrical conditions, one would predict an exponent of 0.67 in the allometric equation for development of length of food-gathering system relative to calyx volume. Observed exponents mostly exceed 0.67, indicating that the food-gathering system generally grows more rapidly than one would expect. Camerate crinoids have several mechanisms for increasing the rate of growth of the food-gathering system: 1) increasing the number of arms; 2) development of biserial from uniserial brachials; 3) increasing the number of brachials and pinnulars; 4) augmenting the heights of brachials and pinnulars; 5) formation of hypertrophied arms; and 6) combining two or more of the above strategies. Although camerate crinoids seem to have maximized the rate of growth of their food-gathering systems as much as possible within the geometrical limits of the structure, the food-gathering ratio (length of food-gathering system/calyx volume) declines throughout ontogeny. Possibly some critical food-gathering ratio serves as a limit beyond which further size increase cannot take place. Obviously, no camerate crinoid reached this limit, although some forms may have approached the critical ratio. Differential natural selection can be documented for several camerate crinoids of Ordovician age. Throughout ontogeny, natural selection reduced variation of length of the food-gathering system relative to calyx volume. Within a single species, natural selection tended to eliminate individuals with relatively short food-gathering systems.

A crinoid endoskeleton shows many supporting relationships because each plate basically supports all of the higher ones. This paper focuses on two supporting relationships. The proximal columnal supports the crown, and the distal fixed brachial bears the arm. In all crinoids examined, the supporting ratio (area of supporting surface/effective weight of structure to be supported) decreases throughout ontogeny indicating that adults are less well "supported" than youngsters. It is possible that critical ratios of (area of supporting brachial/effective weight of food-gathering system) and (area of supporting columnal/effective weight of crown) serve as limits to the maximum size of a camerate crinoid.

The function of a stem is two-fold—elevating the crown above the substrate and flexing the stem which allows the crinoid to reach an advantageous orientation for feeding, shedding sperm into the water, and so forth. During development of the stem, new plates form, some of which are initiated just below the calyx, whereas others are intercalated between older plates. The length of the stem is controlled by the rate of formation of new plates and the rates of height growth of old ones. Accretionary growth of previously formed columnals tends to decrease flexibility of the stem, whereas intercalation of new plates augments flexibility. The ontogeny of a crinoid stem requires a delicate balance between several factors—suitable rate of lengthening, maintenance of the appropriate amount of flexibility, and the development of the appropriate diameter. These factors interact to produce different stems in different species and also to produce different regions within the stem of the same crinoid.

This paper is a tentative and speculative essay on the ontogeny of camerates and, to some extent, living crinoids. The status of work is somewhat analogous to an iceberg where 90 percent of the whole thing is lurking below the murky waters, out of sight and out of mind. Our knowledge of crinoid ontogeny is in a similar state at best with at least 90 percent of the information unseen. At present we have some insight into the development of the geometry of a few living and fossil crinoids and the general functional morphology of crinoid geometry, but little else. Much more work on the geometry, physiology, genetics, and so on of modern crinoids is required before any definitive studies of fossil crinoids can be made. Detailed studies of the ontogeny of flexible and inadunate crinoids are conspicuously lacking. There are few studies which attempt to relate ontogeny and phylogeny although Ubaghs (1958) and Brower (1973, 1974) are exceptions. Little is known of the distribution of different adaptive types in living and fossil crinoids, much less the growth differentials that produce them. However, the worse sin of omission is the lack of knowledge about the genetics of growth in crinoids, not to mention other organisms. Obviously, the development of the geometry of a crinoid is a function of the genetic programming of the animal. Some information is available about the genetics of various organisms, ranging from fruit flies to man. This information yields only a few fleeting insights into the genetics of growth. Yet an understanding of ontogenetic genetics is prerequisite to the unraveling of the geometry. Unfortunately, at present, we can only describe the geometry and speculate, scientifically or otherwise, on the underlying genetic framework.

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